UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PERSISTANCE ET ACTIVITÉ REPRODUCTRICE DES OISEAUX ASSOCIÉS AUX FORÊTS MATURES DANS LES HABITATS RÉSIDUELS EN FORÊT BORÉALE AMÉNAGÉE

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

PAR

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FÉVRIER 2012

AVANT-PROPOS

Ce mémoire est constitué de deux chapitres sous la forme d'articles scientifiques rédigés en anglais. L'introduction et la discussion générale sont rédigées en français. J'ai mené l'ensemble des étapes, de la réalisation de ce projet, de la récolte des données à la rédaction finale, sous la supervision de mes deux directeurs, soit Pierre Drapeau et Daniel Kneeshaw. Il faut mentionner que la mise en place du réseau de stations d'échantillonnage analysée au chapitre I et l'échantillonnage aviaire de 2006 ont été effectués préalablement à mon implication dans le projet. Mes directeurs sont également coauteurs de mes chapitres et y ont apporté commentaires et contributions. Les articles ne sont pas encore publiés, mais devraient être soumis ultérieurement dans les périodiques *Landscape Ecology* et *The Auk*.

La réalisation d'un projet de maîtrise requiert un effort soutenu et une certaine dévotion. Il serait difficile de mener à terme un projet d'une telle envergure sans le soutien et la participation de la famille, amis et collègues. C'est pourquoi je tiens premièrement à remercier Dr Pierre Drapeau, mon directeur de maîtrise, pour m'avoir soutenu et aider à progresser à travers cette grande aventure. Son dévouement et son implication sont louables, compte tenu de son horaire surchargé. Il en va de même avec mon codirecteur, Dr Daniel Kneeshaw, qui m'a prodigué plusieurs conseils constructifs qui me furent très utiles. Je tiens également à mentionner la contribution des autres membres du laboratoire Drapeau tel que, Simon Bédard, Philippe Cadieux, Ugo Ouellette-Lapointe et Tyler Dean Rudolph. À travers des discussions et des échanges, ils m'ont permis de me remettre en questions sur divers aspects de mon travail et m'ont apporté beaucoup de soutien. Il ne faut pas oublier la participation de mes aides de terrains, Vincent Cameron-Trudel, Yan Cosette, Catherine Jetté, Bruno Paré, Mireille Poulin et Sébastien Rioux, sans qui il n'aurait jamais été possible de récolter les données nécessaires à la réussite du projet. Un gros merci à Nathanielle Major et à ma famille pour leur soutien moral et personnel. Mes parents m'ont toujours encouragé à poser des questions, même s'ils ne savaient pas toujours les réponses. Ils m'ont alors poussé à chercher les solutions par moi-même, suscitant ainsi mon goût pour les sciences. Merci également à tous mes amis et collègues du SB-UQAM (2e étage), sans qui les soirées seraient beaucoup plus moroses.

Ce projet a bénéficié des ressources du Centre d'étude de la forêt et de la Chaire industrielle CRSNG-UQAT-UQAM, ainsi que du soutien financier du FQRNT, CRSNG, UQAM et de la Compagnie Abitibi-Bowater.

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RÉSUMÉ

Il a été montré que les oiseaux forestiers sont affectés par leur environnement local, mais également par les caractéristiques du paysage environnant. Ainsi, la structure des communautés des peuplements résiduels de milieux agroforestiers fortement fragmentés peut être altérée par rapport à celles de paysages moins fragmentés. Dans ces milieux, la prédation et le parasitisme par le Vacher à tête brune (*Molathrus ater*) peuvent également affecter le succès de reproduction des oiseaux forestiers des peuplements résiduels. Dans le contexte de paysages forestiers aménagés à des fins de foresterie, il est ainsi possible que la perte d'habitat et la fragmentation influencent également la structure des communautés aviaires ainsi que leur reproduction. Or, les effets de ces deux phénomènes ont jusqu'à maintenant été moins documentés que dans les territoires forestiers modifiés par l'agriculture ou le développement urbain.

Le premier chapitre de ce mémoire analyse la structure et la composition des communautés d'oiseaux dans les habitats résiduels de territoires aménagés, en forêt boréale mixte de la Haute-Mauricie, Québec, Canada. Le deuxième chapitre porte une attention particulière sur l'occupation d'habitat et l'activité reproductrice d'une espèce associée aux forêts matures, le Roitelet à couronne dorée (*Regulus satrapa*). L'objectif est de vérifier les effets des conditions locales et du contexte du paysage sur la composition des communautés aviaires des peuplements résiduels ainsi que sur la densité de territoires, l'activité reproductrice et le succès de nidification des Roitelets à couronne dorée.

Entre 2006 et 2009, des points d'écoute et de la repasse de chants ont permis de répertorier plus de 86 espèces dans 72 stations d'échantillonnage. De plus, le succès d'appariement et d'envol des juvéniles de 59 territoires de Roitelets, distribués dans 14 peuplements résiduels, ont été mesurés à l'aide de la cartographie des territoires et un suivi intensif des groupes familiaux en 2009. Pour les deux études, les données ont été récoltées dans des peuplements résiduels caractérisés par une végétation mature à dominance résineuse et enclavées dans des aires de régénération d'âges variables. Ainsi, certains paysages (1 km de rayon) étaient très jeunes (< 13 % de forêts matures) et d'autres étaient principalement composés de forêts matures (> 78 % de la superficie). L'étude montre que la perte d'habitat mature à l'échelle du paysage ne semble pas affecter significativement les assemblages d'oiseaux des peuplements résiduels, ni la reproduction d'une espèce associée aux forêts matures, le Roitelet à couronne dorée. En effet, la structure des communautés et le succès de reproduction des Roitelets étaient peu variables, peu importe le degré de perte et de fragmentation de l'habitat à l'échelle du paysage. Nous interprétons ce résultat étonnant au fait que la matrice forestière est dominée par de la jeune forêt (7-12 m) qui constitue un milieu qui est vraisemblablement peu hostile aux mouvements des oiseaux forestiers, et ce, malgré le fait qu'il ne subsiste que 10 % du territoire en forêts résineuses matures. Nos résultats indiquent donc que les populations d'oiseaux des forêts matures persistent dans ces environnements fortement fragmentés par la coupe. Cette tolérance à la coupe pourrait être associée aux patrons de coupes en Haute-Mauricie qui, à l'échelle régionale, maintiennent un couvert forestier plus hétérogène (assiettes de coupes plus petites et habitats matures et âgés mieux répartis dans le paysage) que dans d'autres régions aménagées de la forêt commerciale du Québec où les agglomérations de coupes se

juxtaposent sur des milliers de kilomètres carrés. Les habitats résiduels des territoires aménagés en Haute-Mauricie semblent donc avoir une capacité élevée à être utilisés comme habitats-refuges par l'avifaune des forêts matures et âgées.

Mots clés : Oiseaux, perte d'habitat, fragmentation, forêt boréale, paysage aménagé, peuplement résiduel, communautés, succès de reproduction.

INTRODUCTION

L'aménagement forestier a transformé le couvert forestier boréal canadien en une mosaïque de peuplements où les jeunes forêts dominent au détriment des forêts matures et âgées (> 100 ans) (Drapeau *et al.* 2000, Drapeau *et al.* 2003, Bergeron *et al.* 2007). La diminution de ces dernières dans les paysages aménagés fait en sorte qu'elles n'ont pas la capacité de maintenir les communautés animales au niveau rencontré dans les paysages naturels. Plusieurs études ont documenté les diminutions des patrons d'occurrence et d'abondance des populations qui sont associées aux forêts âgées, en territoires aménagés (Thompson *et al.* 1999, Drapeau *et al.* 2003, St-Laurent *et al.* 2008). Bien que certaines espèces puissent profiter ou s'adapter aux nouvelles conditions engendrées par l'aménagement forestier, d'autres, qui présentent un degré plus élevé de spécialisation, sont affectées négativement (Niemi *et al.* 1998, Schmiegelow et Mönkkönen 2002). C'est le cas notamment des espèces associées aux forêts âgées (Imbeau *et al.* 2001, Drapeau *et al.* 2003). Toutefois, la capacité des forêts résiduelles des paysages aménagés à maintenir des populations aviaires aptes à se reproduire, à long terme, a été jusqu'à maintenant très peu documentée. Le présent projet de recherche porte donc à la fois sur la distribution et l'activité reproductrice des oiseaux forestiers des habitats résiduels, en forêt boréale. Plus précisément, ce projet vise à quantifier les changements d'abondance des espèces et de la composition des communautés d'oiseaux dans les forêts résiduelles âgées des paysages aménagés en coupes totales par rapport aux massifs de forêts âgées non récoltés. Dans un deuxième temps, il vise à quantifier l'activité reproductrice d'une espèce associée aux forêts âgées, le Roitelet à couronne dorée (*Regulus satrapa*). Il sera donc possible de déterminer les facteurs importants qui affectent le plus la répartition des espèces, tant à l'échelle locale que du paysage, et de mesurer leur activité reproductrice au sein des habitats résiduels. Une attention particulière est portée sur l'âge et la hauteur moyenne des perturbations du paysage adjacent aux habitats résiduels afin de vérifier si la maturité du paysage peut avoir un effet sur les oiseaux des peuplements résiduels. L'industrie forestière pourra ainsi utiliser ces résultats pour évaluer comment leurs pratiques permettent ou non de maintenir des populations d'oiseaux aptes à se reproduire dans ces habitats résiduels.

La forêt boréale de l'est de l'Amérique du Nord est caractérisée par une mosaïque de grandes étendues de forêts matures continues, parsemées par des peuplements isolés en régénération. Cet écosystème est maintenu par la dynamique des perturbations qui y adviennent. Historiquement, elles étaient naturelles, le feu étant la plus importante avec les épidémies d'insectes (Bonan et Shugart 1989, Bergeron et Leduc 1998, Bergeron *et al.* 2001). Toutefois, l'aménagement industriel des dernières décennies a transformé le couvert forestier de manière plus soutenue et plus extensive que les perturbations naturelles (Spies *et al.* 1994, Wallin *et al.* 1994, McRae *et al.* 2001). Dans le cas de la forêt boréale de l'est de l'Amérique du Nord, l'aménagement effectué jusqu'à maintenant a engendré un rajeunissement des paysages (Hagan *et al.* 1997, Harper et Macdonald 2002, Bergeron *et al.* 2007). Un changement de la composition des espèces d'arbres a même été observé en forêt boréale mixte du Québec, où il semble y avoir une augmentation des arbres décidus (Carleton et MacLellan 1994, Bergeron et Harvey 1997) et un changement de la composition des communautés d'oiseaux (Drapeau *et al.* 2000). Or, nous avons très peu de connaissances concernant la capacité de maintien de la biodiversité de la mosaïque hétérogène ainsi créée (Bergeron *et al.* 2007). Les impacts de la foresterie sur cette mosaïque sont difficiles à cerner, car il n'existe pas de frontières nettes entre les différents peuplements; chacun possédant des caractéristiques propres différentes en terme de qualité d'habitat (Bunnell *et al.* 1999, Schmiegelow et Mönkkönen 2002, Guénette et Villard 2005).

Communautés aviaires

Les oiseaux représentent le groupe taxinomique le plus riche des vertébrés de la forêt boréale avec plus de 70 % de tous les vertébrés terrestres (Mönkkönen et Viro 1997). Trois grands groupes d'oiseaux utilisent la forêt boréale pour se reproduire : les migrateurs de longue distance qui passent l'hiver dans les tropiques (50-55 % des oiseaux boréaux), les migrateurs de courte distance qui demeurent l'hiver dans les zones tempérées (30-36 %) et les résidents permanents (8-20 %) (Erskine 1977). Il y a donc environ 80 % de la communauté aviaire boréale qui est migratrice. Or, il y a une plus grande proportion de migrateurs dans les vieilles forêts nord-américaines que dans les jeunes peuplements issus d'un feu ou de la coupe forestière (Monkkonen et Helle 1989). Depuis quelques décennies, plusieurs travaux ont montré une diminution des migrateurs de longue distance qui se reproduisent en forêt tempérée en Amérique du Nord (Robbins *et al.* 1989, Terborgh 1989,

Askins *et al.* 1990). Celle-ci serait principalement due à la fragmentation et la perte d'habitats forestiers résultant du développement de l'agriculture et de l'urbanisation, tant dans les lieux d'hivernage que de reproduction (Robinson et Wilcove 1994, Askins 1995, Robinson *et al.* 1995, Flather et Sauer 1996, Rappole 1996). En forêt boréale, toutefois, plusieurs espèces résidentes utilisent la forêt mature à cause de la grande quantité d'arbres-morts, dont ils se servent pour se nourrir et nicher (Imbeau *et al.* 2001). Ces oiseaux sont reconnus pour avoir une aire de répartition et un territoire imposant, d'être associés à des habitats spécifiques et d'avoir de petites populations locales. Vraisemblablement, ils peuvent être affectés davantage par les modifications de leur habitat que ne le sont les migrateurs (Imbeau *et al.* 2001, Schmiegelow et Mönkkönen 2002).

Les oiseaux sont des acteurs très importants des écosystèmes boréaux. Beaucoup d'entre eux sont insectivores. Or, plusieurs études, dont fait mention la revue de littérature de Holmes (1990), ont montré qu'ils contrôlent les populations d'insectes, tant qu'il ne s'agit pas d'une épidémie. Dans le même sens, leur prédation sur la tordeuse du bourgeon de l'épinette (*Choristoneura fumiferana*) permettrait de réduire la sévérité des épidémies (Holling 1988, Crawford et Jennings 1989).

En vertu de leur diversité, les oiseaux utilisent la diversité structurale (horizontale comme verticale) du couvert forestier. Ils sont donc très sensibles aux modifications de la structure de leur habitat. C'est pourquoi Furness et Greenwood (1993) proposent d'utiliser les oiseaux comme indicateurs de la santé d'un écosystème. Il est connu que les espèces aviaires réagissent aux changements de la végétation locale (James et Wamer 1982, Cody 1985, Bibby et Burgess 2000). En Europe, les changements de la composition des espèces d'arbres et ses impacts sur les communautés aviaires ont la réputation d'être les plus grandes perturbations liées à la foresterie (Swenson et Angelstam 1993, Enoksson *et al.* 1995, Edenius et Elmberg 1996). Il en va de même en Amérique du Nord où des études ont montré que la composition des communautés aviaires est affectée par la perte de couvert forestier mixte constitué d'un mélange d'essences résineuses et feuillues à l'échelle du peuplement (Bayne et Hobson 1997) ainsi qu'à l'échelle du paysage (Drapeau *et al.* 2000). Dans son étude, Gram et al. (2003), concluent que les activités forestières affectent la densité des espèces d'oiseaux associées aux forêts résiduelles matures et ces effets peuvent durer plus de trois ans. En exploitant principalement les vieilles forêts, la foresterie

affecte négativement les oiseaux spécialistes de ce milieu et favorise l'expansion des espèces associées aux milieux ouverts ou de jeunes forêts (Drapeau *et al.* 2000, Imbeau *et al.* 2001, Schmiegelow et Mönkkönen 2002). C'est donc dans cette lignée de travaux récents centrés sur le déclin des populations d'oiseaux forestiers et leur sensibilité à la perte et à la fragmentation des forêts matures par la foresterie que s'inscrit le présent mémoire.

Réglementation de la foresterie

Pour limiter les impacts environnementaux et la fragmentation du milieu, le Gouvernement du Québec a instauré diverses modalités d'aménagement dans la réglementation qui régissent les interventions forestières. Il a d'abord instauré la coupe avec la protection de la régénération et des sols (CPRS). Contrairement à la coupe totale, la CPRS s'effectue en limitant les déplacements de la machinerie de manière à ce que les sentiers de débardage couvrent un maximum de 25 % de l'assiette de coupe. Cela limite les dommages à la régénération préétablie et minimise le compactage du sol. Depuis 1996, les parterres de coupes ne peuvent excéder une superficie de 150 ha (250 ha entre 1988 et 1995) et doivent être isolés par des séparateurs de coupe d'une largeur de 60 ou 100 m selon la taille des coupes adjacentes. De plus, une bordure d'un minimum de 20 m doit être conservée sur le pourtour des lacs, de chaque côté des cours d'eau et des routes principales (Potvin et Bertrand 2004, Ferron et St-Laurent 2005, Ministère des Ressources Naturelles et des Forêts 2009). Les séparateurs de coupe, les bandes riveraines et les milieux inaccessibles (ex.: pente ≥ 40 %) constituent les principales forêts résiduelles du territoire boréal québécois.

Rôles des peuplements résiduels

Les peuplements résiduels jouent des rôles écologiques importants. Premièrement, ils servent de refuge aux oiseaux délocalisés lors des traitements forestiers (Hagan et Johnston 1992, Andrén 1994, Schmiegelow *et al.* 1997, Debinski et Holt 2000). Puis, ils favorisent la recolonisation des milieux exploités en agissant comme source potentielle d'individus et d'espèces (Venier et Pearce 2005). Selon leur configuration, ils peuvent servir de corridor de déplacement (Machtans *et al.* 1996, Debinski et Holt 2000, Robichaud *et al.* 2002). Ils constituent également une source de graines pour le reboisement des parterres de coupe (Eberhart et Woodard 1987). Tous ces éléments confirment le fait que les peuplements résiduels contribuent à la complexité structurale du milieu qui est associée avec

sa productivité et sa biodiversité (Hansen *et al.* 1991, Schieck et Hobson 2000). De ce fait, les peuplements résiduels ont une grande importance pour les communautés écologiques.

Échelles d'étude

Échelle locale

Il est de plus en plus reconnu que les oiseaux sont influencés à plusieurs échelles de leur environnement (Wiens et Rotenberry 1981, Orians et Wittenberger 1991, Donovan *et al.* 1997, Drapeau *et al.* 2000). Celle qui fut, jusqu'à maintenant, la plus étudiée est l'échelle locale. Les conditions locales des habitats immédiats ont souvent été utilisées pour expliquer la répartition des individus de différentes espèces. Dans plusieurs études multi-échelles, l'influence de l'échelle locale (peuplement) était non négligeable et parfois la plus importante (Pearson 1993, Drapeau *et al.* 2000, Hobson *et al.* 2000, Lichstein *et al.* 2002).

Les principales variables locales qui influencent les oiseaux sont la structure verticale, la densité de la végétation, la composition du couvert (conifères ou feuillus) et la quantité de bois mort (c.f.: Bibby et Burgess 2000). Une augmentation de la structure verticale de la végétation semble provoquer un accroissement de la diversité aviaire (MacArthur et MacArthur 1961, Willson 1974, Venier et Pearce 2005, Askins *et al.* 2007). Cela serait dû à une hausse potentielle de la quantité d'habitats disponibles (James et Wamer 1982). Dans le même sens, plusieurs études ont montré que l'abondance des espèces de forêts matures est positivement corrélée avec la densité d'arbres et l'inverse, dans le cas des espèces de milieu ouvert (Hansen *et al.* 1995, Schieck et Hobson 2000, Tittler *et al.* 2001, Stuart-Smith *et al.* 2006). D'autres travaux ont montré que la quantité de conifères, en termes de densité ou de couverture, est une variable significative qui explique la présence de certaines espèces aviaires (Drapeau *et al.* 2000, Lee *et al.* 2002, Betts *et al.* 2006, Stuart-Smith *et al.* 2006). Tout au long de son vieillissement, la forêt boréale accumule de la matière morte ou sénescente. Or, cette dernière représente un attribut fonctionnel très important pour le maintien de la diversité aviaire, qu'elle soit sur pied ou au sol (c.f.: Drapeau *et al.* 2003). D'ailleurs, le bois mort et sénescent est corrélé avec la présence de certaines espèces d'oiseaux en forêt boréale (Drapeau *et al.* 2000, Venier et Pearce 2005).

Échelle de l'îlot forestier

L'échelle de l'îlot forestier intègre des paramètres tels que la taille et la forme. Peu d'études ont évalué l'influence de la taille de l'îlot forestier sur les communautés animales en forêt boréale (Boulet *et al.* 2003). L'aire de l'îlot est critique au maintien des communautés animales forestières. Considérant que les individus nécessitent un territoire minimal pour leur survie, les peuplements résiduels ne peuvent donc pas être de taille inférieure aux territoires des individus. Toutefois, certains oiseaux peuvent utiliser plusieurs îlots et le territoire adjacent pour combler leur besoin territorial (Andrén 1994, c.f.: Schmiegelow et Mönkkönen 2002). Dans une revue de la littérature, Schmiegelow et Mönkkönen (2002) ainsi que Debinski et Holt (2000) spécifient que la diversité des communautés des peuplements résiduels semble être corrélée avec la taille des îlots, mais les résultats concernant l'abondance (voir : Lee *et al.* 2002) et la reproduction des individus ne sont pas concluants (Paton 1994, Huhta *et al.* 1998). En forêt boréale mixte de l'Ouest du Canada, l'étude de Schieck et Hobson (2000) montre que plus les peuplements résiduels sont âgés et grands, plus la communauté aviaire est composée d'espèces associées aux forêts matures. La forme des peuplements est également à considérer : plus ils sont découpés (c.-à-d. un grand ratio bordure/habitat d'intérieur), plus il y a de bordures et plus ils peuvent être affectés par les effets de la fragmentation (Manolis *et al.* 2002, Askins *et al.* 2007).

Échelle du paysage

Troisièmement, pour savoir si les peuplements résiduels remplissent bien un rôle de refuge ou de corridor de déplacements, il faut s'intéresser à leur arrangement spatial et à leur environnement adjacent. Pour ce faire, il est important de considérer la composition et la configuration du paysage environnant les habitats résiduels (Mazerolle et Villard 1999, Bergeron *et al.* 2007). D'ailleurs, plusieurs études ont montré que cette échelle était aussi importante que les conditions locales pour expliquer l'occurrence et l'abondance des oiseaux (Hagan *et al.* 1997, Drapeau *et al.* 2000, Penhollow et Stauffer 2000). Son importance relative a souvent été associée à la quantité d'habitats de qualité présents dans le paysage et à l'échelle régionale (Robinson *et al.* 1995, Schmiegelow et Mönkkönen 2002). Cette variabilité explique pourquoi l'importance de cette échelle est si variable d'une étude à une autre (c.f.: Lichstein *et al.* 2002). Plusieurs variables décrivant la configuration et la composition du paysage peuvent être utilisées lors des analyses sur les populations aviaires.

Or, le choix de ces variables, l'échelle, les analyses utilisées et le type de paysage (agricole/forestier, peu/hautement fragmenté) ont une grande importance sur les résultats des analyses et surtout sur leur interprétation écologique dans la structure et la composition des communautés aviaires.

La configuration et la composition du paysage peuvent influencer le succès reproducteur des oiseaux, soit en agissant sur le taux de prédation au nid ou sur le taux de parasitisme. Par exemple, plus le paysage est fragmenté, plus il semble y avoir de la prédation de nids (Andrén 1995, Robinson *et al.* 1995, Donovan *et al.* 1997, Thompson III *et al.* 2000). Ces dernières études ont principalement été réalisées en milieu agricole. Cependant, Tewksbury et al. (1998) sont parvenus à des résultats inverses en milieu forestier. Certaines de ces études ont également trouvé qu'il y a moins de parasitisme de la part du Vacher à tête brune si le couvert forestier, à l'échelle du paysage, est important (Robinson *et al.* 1995, Tewksbury *et al.* 1998). L'environnement adjacent influence également le déplacement des individus des espèces forestières entre les îlots forestiers et ainsi, leur possibilité de dispersion et de colonisation (Fahrig et Merriam 1994, c.f.: Robichaud *et al.* 2002). En effet, les oiseaux circulent significativement moins dans les ouvertures que dans les milieux forestiers, tant en été (Desrochers et Hannon 1997), qu'en hiver (St-Clair *et al.* 1998).

Les principales variables qui décrivent les caractéristiques du paysage et qui affectent les communautés aviaires sont : la composition du paysage (la proportion de conifères ou de feuillus dans le paysage) (Drapeau *et al.* 2000, Lee *et al.* 2002, Betts *et al.* 2006), la densité et la structure du couvert forestier (Drapeau *et al.* 2000) et la nature du paysage (c.-à-d. : milieu agricole, forestier, résidentiel, etc.) (Drapeau *et al.* 2000, Heikkinen *et al.* 2004). Pour ce qui est de la configuration, plusieurs variables ont été testées dans un bon nombre d'études en milieu forestier (quantité de forêt intérieure, quantité de bordure, relief des bordures, hétérogénéité du paysage, etc.), mais leur influence sur les communautés est, en général, négligeable ou peu significative (McGarigal et McComb 1995, Drapeau *et al.* 2000, Lichstein *et al.* 2002).

Plusieurs études ont montré que la relation entre les populations d'oiseaux et la perte d'habitat dans le paysage n'est pas nécessairement linéaire. En effet, il y a des situations auxquelles la perte d'habitat n'est pas capable d'expliquer seule le déclin de certaines

populations. La fragmentation peut avoir une influence notable à partir d'un certain seuil de perte d'habitat dans le paysage (Andrén 1994, Fahrig 1997, Mönkkönen et Reunanen 1999, Betts *et al.* 2007). Selon Andrén (1994), le couvert forestier doit être inférieur à 30 % pour que la configuration du paysage soit significativement importante. Toutefois, cette revue de la littérature repose sur des études principalement européennes dont peu étaient réalisées en milieu forestier au moment où Andrén (1994) a réalisé cette méta-analyse. La configuration du paysage s'est souvent révélée significative en milieu agricole; peu d'études l'ont toutefois observé en milieu forestier (Mönkkönen et Reunanen 1999, Schmiegelow et Mönkkönen 2002). En forêt décidue, Betts et al. (2007) ont trouvé que l'occurrence des oiseaux peut changer abruptement lorsque la quantité d'habitats dans le paysage varie de 9 à 29 %, selon les espèces.

Fragmentation et effet de bordure

Deux phénomènes ont lieu à l'échelle du paysage : la perte d'habitat et la fragmentation. La perte d'habitat renvoie à la modification d'un territoire le rendant inhospitalier à sa fréquentation par les organismes associés aux habitats résiduels d'origine. En général, il en résulte la perte d'individus et la diminution de leur population. Ces effets peuvent être accentués par la fragmentation de l'habitat, qui se traduit par des effets dus à la configuration des habitats résiduels tels que les interactions biologiques accrues aux bordures des habitats résiduels (effets de bordure), l'extirpation des espèces à plus grands domaines vitaux (effets de taille) et une dispersion réduite des organismes (effet d'isolement et de diminution de la connectivité) (Andrén 1994, McGarigal et McComb 1995, Bender *et al.* 1998, Villard *et al.* 1999, Schmiegelow et Mönkkönen 2002, Heikkinen *et al.* 2004). L'amplitude des effets de la fragmentation dépend des espèces, mais également de la quantité d'habitats de qualité à l'échelle du paysage. Les effets de la configuration des habitats résiduels semblent être plus importants lorsque le paysage est très fragmenté (Betts *et al.* 2006).

L'industrie forestière est l'une des sources de fragmentation par la création de bordures en milieu forestier. L'effet de bordure peut influencer négativement le taux de survie et de reproduction des communautés animales et même occasionner une diminution des populations locales et régionales (Robinson *et al.* 1995, Donovan *et al.* 1997). Il a été montré qu'il peut réduire le taux d'appariement des oiseaux (Gibbs et Faaborg 1990, Porneluzi *et al.*

1993, Villard *et al.* 1993, Hagan *et al.* 1996, Bayne et Hobson 2001). Il peut influencer la quantité d'arthropodes présents et donc, potentiellement limiter les populations d'insectivores (Burke et Nol 1998, Whitaker *et al.* 2000, Zanette *et al.* 2000, Harris et Reed 2002). L'existence d'un effet de bordure prononcé en forêt boréale est mitigée. En effet, plusieurs études appuient sa présence en paysage agricole. Toutefois, peu sont parvenus à des résultats significatifs en milieu forestier (c.f.: Andrén 1995, Schmiegelow et Mönkkönen 2002, Batáry et Báldi 2004). Par exemple, Cotterill et Hannon (1999) n'ont pas trouvé de hausse de la prédation sur des nids artificiels placés dans des peuplements résiduels, une à cinq années après les interventions forestières.

Séparateurs de coupes

L'effet de bordure exerce une influence sur les caractéristiques physiques des peuplements résiduels en forêt boréale sur une distance variant de 5 à 60 mètres de l'interface coupe-habitat résiduel (Esseen et Renhorn 1998, Harper et Macdonald 2002, Harper *et al.* 2004, Mascarúa López *et al.* 2006). Toutefois, plusieurs études mentionnent que cet effet peut s'étendre à l'intégralité de séparateurs de coupe d'une largeur de 50 ou 60 m (Mascarúa López *et al.* 2006). Cela pourrait expliquer les résultats de Ferron et St-Laurent (2005) et de Potvin et Bertrand (2004) qui ont montré que les séparateurs de coupes de 60 à 100 m sont peu efficaces pour conserver certaines espèces fauniques forestières. Les séparateurs de coupe de 60 m présentent un taux d'appariement des espèces d'intérieur moindre que celui de massifs forestiers matures (Boulet *et al.* 2003). Le taux de prédation des nids ne semble pas en être la cause puisqu'il n'y est pas plus élevé (Boulet *et al.* 2003). En se basant sur le taux d'appariement et la taille des territoires de Paruline couronnée (*Seiurus aurocappillus* L.), Lambert et Hannon (2000) montrent qu'il n'y a plus d'effet de lisière dans des séparateurs de coupe de 100 et 200 m.

Bandes riveraines

Les bandes riveraines ne semblent pas toujours constituer un habitat adéquat pour les espèces aviaires généralement associées aux forêts matures (Whitaker et Montevecchi 1999, Boulet *et al.* 2003). En effet, contrairement aux bandes de 60 m, celles de 20 et 40 m semblent être inaptes à maintenir les populations aviaires forestières (Darveau *et al.* 1995). Pourtant, Boulet et al. (2003) ont montré que les bandes de 60 m ne parvenaient pas non

plus à les maintenir. Pour ce qui est du succès reproducteur, les bandes de 40 et 60 m ont même présenté un taux de prédation sur des nids artificiels, plus élevé que celles de 20 m et que les massifs forestiers témoins (Darveau *et al.* 1997). Ces dernières seraient même évitées de la part des principaux prédateurs des nids (c.-à-d. écureuils et petits mammifères) (Darveau *et al.* 2001). Pour leur part, Boulet et al. (2003) ont trouvé des taux de prédations semblables entre les bandes riveraines de 60 m et des massifs témoins. Cela pourrait être dû au fait que l'effet de bordure n'affecte pas la totalité des bandes riveraines (Mascarúa López *et al.* 2006).

Importance du suivi de l'activité reproductrice

Il est important de vérifier si les oiseaux associés aux forêts matures et âgées des milieux aménagés défendent des territoires et accomplissent des activités de reproduction dans les habitats résiduels. L'activité de reproduction n'est pas toujours corrélée à l'abondance des individus reproducteurs (Van Horne 1983, Purcell et Verner 1998). Il est alors important de vérifier si les peuplements résiduels montrent des activités de reproduction chez les espèces d'oiseaux inféodées aux forêts matures et âgées en plus d'étudier la structure de la communauté. Le Roitelet à couronne dorée (*Regulus satrapa*) est ciblé dans le cadre de nos travaux sur les activités reproductrices, car il s'agit d'une espèce associée aux forêts matures et âgées. D'ailleurs, nos inventaires précédents en forêt mature et âgée résiduelle ont montré que cette espèce était l'une des plus fréquentes sur le territoire étudié (occurrence de 78 % dans les points d'écoute). De plus, cette espèce est très sensible au rajeunissement de son habitat (Guénette et Villard 2005, Venier et Pearce 2005, Stuart-Smith *et al.* 2006, St-Laurent *et al.* 2008). Ces caractéristiques en font une espèce intéressante pour étudier l'effet de refuge biologique joué par les forêts âgées résiduelles dans les territoires aménagés caractérisés par un rajeunissement du couvert forestier à l'échelle du paysage.

Objectifs et hypothèses

Ce mémoire porte sur l'étude des variations de la composition et de la structure des communautés aviaires et de l'activité reproductrice d'une espèce de forêt mature dans les peuplements résiduels boréaux. Ces travaux sous-tendent la prise en compte de plusieurs échelles spatiales dans l'analyse de la réponse de l'avifaune quant à l'occupation et

l'utilisation des habitats résiduels. Le premier objectif de mémoire consiste à déterminer l'importance relative des diverses échelles spatiales (c.-à-d. : échelle locale, de l'îlot forestier et du paysage) sur la structure des communautés d'oiseaux et l'activité reproductrice d'espèces associées aux forêts âgées. De cette manière, il sera possible de déterminer si le contexte adjacent des peuplements résiduels peut influencer la structure des communautés ou l'activité reproductrice de l'avifaune qui s'y trouve. Deuxièmement, il vise à déterminer les variables environnementales qui affectent de manière significative la structure des communautés aviaires, ainsi que l'activité reproductrice d'espèces associées aux forêts âgées.

La présence de peuplements résiduels dans les paysages aménagés contribue à augmenter la diversité d'habitats à l'échelle du paysage. De ce fait, les peuplements résiduels deviennent des habitats potentiels pour une plus grande diversité d'espèces aviaires. Un rajeunissement du paysage peut permettre l'établissement d'espèces plus fréquemment associées aux jeunes forêts ou aux milieux ouverts. Dans un contexte de raréfaction de la forêt mature et âgée, on peut se demander si les peuplements résiduels continuent d'être des habitats satisfaisants pour les espèces associées aux forêts matures et âgées. Ainsi, nous prévoyons que les peuplements résiduels se trouvant dans de jeunes paysages devraient avoir une structure de communauté aviaire différente de celle de massifs forestiers matures et qu'ils devraient supporter moins de couples nicheurs et un moins bon succès reproducteur chez ces derniers.

CHAPITRE I

CAN MATURE FOREST REMNANTS MAINTAIN SONGBIRD COMMUNITIES IN LANDSCAPES HIGHLY FRAGMENTED BY TIMBER HARVESTING IN THE BOREAL MIXED CONIFER-HARDWOOD FOREST?

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1.1 Abstract

It was shown that habitat loss at the landscape scale caused by timber harvesting could affect populations of several bird species associated with mature forests. We assessed how the composition and structure of songbird communities are maintained in mature forest remnants of landscapes highly fragmented (12% of mature coniferous forest habitat remaining in 4 000 km^2 area) by timber production in the boreal mixed conifer-hardwood forest of eastern Canada. We tested the prediction that bird assemblages in mature forest remnants surrounded by low amounts of mature forest habitat (within 500 m and 1-km radius) would harbor fewer mature forest associates than remnants surrounded by high amounts of mature forest. Between 2006 and 2009, 72 stations were sampled in forest remnants characterized by a mature conifer forest cover and embedded (1-km radius) in regenerating landscapes with different amounts of mature forest (5-78% of the landscape). Sampling stations were randomly selected to cover this gradient of mature forest habitat and were sampled for three years. Point counts and song playbacks allowed us to identify over 86 species in residual stands. The majority of detections (67 %) were associated with 32 species considered to be dependent on mature forests. Bird community composition in our sampling stations was consistently dominated by mature forest species even though slight annual variation occurred in their abundances over the three years of sampling. We then analyzed the effects of local conditions and landscape composition on avian communities in these remnants. We found that the composition and structure of the studied bird communities were not altered by the amount of mature forest habitat nor by the amount of early-seral habitat in adjacent 500 m and 1-km landscapes. Thus, we conclude that bird communities in remnant mature forest stands were tolerant to strong variations in the amount of mature forest habitat at those neighboring landscape scales (500 m and 1-km radius) and this in a regional context of low mature and old forest cover. We discuss the persistence of bird assemblages in mature and old forest remnants with regards to changes in the age structure of the forest cover at the landscape scale. We suggest that the increasing importance of young forest cover in these even-aged managed landscapes may not limit forest bird movements, dampening the effects of mature habitat loss and fragmentation.

Keywords: Songbird communities, habitat loss, fragmentation, managed landscape, forest remnants, boreal forest

1.2 Introduction

In recent years, several studies have shown that, in addition to local habitat conditions, birds respond to the characteristics of the surrounding landscape (Andrén 1994, McGarigal and McComb 1995, Robinson *et al.* 1995, Edenius and Elmberg 1996, Schmiegelow *et al.* 1997, Drapeau *et al.* 2000). Although the relationship between local environmental variables and bird populations is well documented, less is known about the influence of the matrix at the landscape-scale. The composition and structure of the landscape can both influence songbird assemblages and individual species abundance (Hagan *et al.* 1997, Drapeau *et al.* 2000, Penhollow and Stauffer 2000, Lichstein *et al.* 2002, Askins *et al.* 2007) as well as their reproductive success (Andrén 1995, Robinson *et al.* 1995, Bayne and Hobson 1997, Cotterill and Hannon 1999, Stephens *et al.* 2004). These relationships have been well documented in forest remnants in agro-forested landscapes where forest-dwelling birds decrease in abundance as a function of patch properties such as forest size and shape (Whitcomb *et al.* 1981a, Robbins *et al.* 1989) and experience a lower reproductive success than birds living in continuous forest landscapes (Andrén 1995, Robinson *et al.* 1995, Hobson and Bayne 2000). Hence, bird populations' declines in such systems are linked to the combined reduction in forest cover (habitat loss) and the effects of the spatial configuration of remnant suitable habitat (patch size, edge effects) on forest birds (habitat fragmentation) in the landscape.

In boreal landscapes managed for timber production, studies undertaken on the effects of habitat loss and fragmentation on birds have shown that the effects of habitat fragmentation are far less important than net habitat loss (Andrén 1994, Drolet *et al.* 1999, Drapeau *et al.* 2000, Schmiegelow and Mönkkönen 2002). More specifically, studies that have documented songbird diversity and abundance patterns in forest remnants of timber managed landscapes have shown that birds are significantly more influenced by the immediate landscape composition (amount of old forest vs. amount of clearcuts) or local habitat conditions of remnants depending on the considered species or studies than by configuration of remnant habitat (amount of edges, isolation from other forest tracks) or patch properties such as size and shape (Darveau *et al.* 1995, McGarigal and McComb 1995, Schmiegelow *et al.* 1997, Drolet *et al.* 1999, Drapeau *et al.* 2000, Hannon and Schmiegelow 2002).

Most of the studies conducted in boreal forests that are managed for timber harvesting (see Andrén 1994, Schmiegelow and Mönkkönen 2002) found that birds are more influenced by the local characteristics of the remnants rather than landscape characteristics. (see Andrén 1994, Schmiegelow and Mönkkönen 2002). The weak evidence for fragmentation effects on birds in these ecosystems has often been interpreted with regards to three hypotheses. First, boreal bird species may be not affected by harvesting because they are adapted to live in a boreal landscape mosaic of habitats affected by large-scale natural disturbances (i.e.: fire and insect outbreaks) under which bird populations have evolved resilience mechanisms (Hagan and Johnston 1992, Niemi *et al.* 1998, Schmiegelow and Mönkkönen 2002). Second, forested landscapes managed for timber production are dynamic, generating a mosaic of forest cover types of different seral stages (Schmiegelow and Mönkkönen 2002). Managed boreal forests are not sharply divided between simple forest and non-forest habitats. Forest disturbances, such as harvesting, thus promote the creation of temporary edges that are less sharp and for which edge-related effects on birds may be less severe than in agro-forested landscapes (Rudnicky and Hunter 1993b, Rudnicky and Hunter 1993a, Bayne and Hobson 1997). Whereas the harvested forest matrix is hostile to forest-dwelling bird movements immediately following harvesting (Desrochers and Hannon 1997, Rail *et al.* 1998, Bélisle and Desrochers 2002, Bélisle and St. Clair 2002), they are quickly able to move and disperse in regenerating areas when the trees reach the sapling stage (2 to 7 meters) (Imbeau *et al.* 1999, Norton *et al.* 2000, Robichaud *et al.* 2002, St-Laurent *et al.* 2008). Hence, contrary to agro-forested landscapes, forest management in boreal ecosystems does not lead to permanent landscape configurations but rather to dynamic changes of the spatial configuration of habitats at the landscape scale. Third, empirical and theoretical models have shown that effects of habitat fragmentation that exacerbate population declines to a level which may lead to local extinction, occur at certain thresholds, i.e. when the amount of suitable habitat becomes less than 20 to 30 % (Andrén 1994, Fahrig 1997). Similarly, Betts *et al.* (2007) found in timber managed landscapes in northern hardwood forests of New Brunswick that the occurrence of songbirds can change abruptly with the amount of suitable habitat in the landscape. They identified species-specific thresholds varying between 9 and 29 % of suitable habitat. Empirical studies undertaken up to now in boreal forest landscapes managed for timber harvesting have mostly been done in environments where managed and unharvested forest landscapes are nearby generating regional forest conditions where the forest cover is rarely below the above suitable habitat

thresholds (McGarigal and McComb 1995, Edenius and Elmberg 1996, Schmiegelow *et al.* 1997, Drolet *et al.* 1999, Drapeau *et al.* 2000, Lichstein *et al.* 2002, Brotons *et al.* 2003). Hence, the regional amount of unharvested forest may hamper the configuration effects on birds in nearby managed forest landscapes.

In this paper, we document the persistence of bird assemblages in mature and old forest remnants in the eastern Canadian boreal forest. More closely, in a region where mature forests are highly fragmented by timber harvesting and where the long management history has transformed the matrix into dominating early-seral and young forest stages. This provided the opportunity to conduct a field experiment to test the response of mature forest birds to habitat loss and fragmentation along a gradient of mature forest fragmentation at the landscape scale in a regional context where the amount of mature forests falls below suitable habitat thresholds mentioned before. We predict that the numerical importance of mature forest birds (both the number of species and their relative abundance) will decrease in forest remnants where landscape contexts are characterized by a low percent cover of mature forest. This prediction will allow to evaluate the occurrence of landscape-scale thresholds of habitat loss at which bird populations may be affected.

1.3 Methods

1.3.1 Study region

Our study area is located in the upper part of the Mauricie region, Quebec, Canada (47°53'N, 72°53'W) (figure 1.1). This 4 000 km^2 forest management unit is mainly under industrial timber management (68 % of the area) (Levac 2008). It is part of the balsam fir (*Abies balsamea*) — white birch (*Betula papyrifera*) bioclimatic domain of the boreal mixed wood forest (Robitaille and Saucier 1998). Forest dynamics are now primarily driven by logging activities and natural disturbances (i.e.: fire and insect outbreaks). The region has one of the longest harvesting histories in Quebec. Fire history reconstruction shows that the fire cycle is longer than even-aged management rotations implying that the forest cover at the regional scale was dominated by overmature and old-growth stands which contrast with current composition of forest cover types (Bergeron *et al.* 2001, Lesieur *et al.* 2002). Hence, since the beginning of the 20th century the regional forest matrix has shifted from a landscape dominated by mature and old forest to a younger deciduous landscape (Alvarez 2009).

Because of the region's undulating relief, some areas are inaccessible for timber harvesting. Hence, about 10% of the studied region still contains mature mixed-conifer forest.

1.3.2 Study design

Natural succession in boreal mixedwoods typically proceeds from early dominance by shade intolerant hardwoods to mixed hardwood conifer dominance to dominance by shade tolerant conifers (Bergeron and Dubuc 1988). In our study area, we controlled for local forest conditions by sampling mixed-conifer mature remnants with similar characteristics (≥ 50 years old, > 12 m in height with > 40% canopy closure and dominated by conifer > 50 %) and embedded in different landscapes that were harvested along a time since harvest gradient. Mixed-conifer mature remnants were chosen because they are representative of old forest conditions in our study region. Seventy-two sampling stations were located in the selected remnants. Remnants and stations were chosen to maximize the variation in the amount of mature forest cover within one kilometer, from a highly fragmented landscape (5 % of mature forests), to a weakly fragmented one (78 % of mature forest). In addition, remnants were located close to roads (< 500 m) to facilitate access and were large enough (> 5 ha) to contain point counts of a radius of 75 m. Stations were separated by a minimum distance of 200 m. Martin *et al.* (1997) suggest this distance to ensure the independence of songbird point counts. To avoid a crowding effect, which occurs in remnant habitats near recent cutover areas (Hagan and Johnston 1992, Andrén 1994, Darveau *et al.* 1995, Schmiegelow *et al.* 1997), the selected remnants were embedded in harvested areas older than 5 years old. Analysis of forest landscapes and selection of sampling stations and remnants were conducted using GIS analysis of digital forestry maps based on aerial photographs (Quebec Ministry of Natural Resources and Wildlife) with ArcGIS software (ESRI).

1.3.3 Bird sampling

Bird sampling was conducted during the 2006, 2008 and 2009 breeding seasons, between the end of May and beginning of July. Bird count sample points were visited three times in 2008 and 2009 and two times in 2006. Sampling was conducted from dawn until 10:00, a time frame during which birds are highly active. At each station, meteorological conditions (wind speed, precipitation and cloud cover) were noted. If the wind exceeded

8 km/h or if it rained, sampling was deferred, because the detection capacity of the observers could be reduced (Drapeau *et al.* 1999, Bibby and Burgess 2000).

Fixed-radius point counts (75 m) were used to sample bird communities at each station. This method is appropriate to sample bird species that are easily detectable in environments where movement of observers is limited (Bibby and Burgess 2000). Point counts with a fixed-radius were used in order to limit bird detections to individuals detected within the sampled remnants. In 2008 and 2009, point counts lasted 15 minutes for a total sampling effort of 45 minutes per station per year. In 2006, the count duration was 20 minutes (for a total sampling effort of 40 minutes). All the visual or auditive detections of birds were noted during three — five minutes intervals (four in 2006) at each visit. Detections within and outside the 75 m radii were noted separately. Individual birds were counted once during each 5-min interval (Drapeau *et al.* 1999, Bibby and Burgess 2000). Birds that flew over the sampling station were not counted. Analyses were done using the total number of individuals per species per station, which corresponds to the maximum abundance of individuals detected across the 2 or 3 visits.

The detection of some species, mostly resident birds, is not always effective because of their large territories or their discreet behavior (Potvin and Bertrand 2004). This is the case for woodpeckers (*Picidae*). Song playbacks were thus used to allow their detection and the detection of four additional species associated with mature forests and sensitive to habitat loss. Hence, in addition to point counts we conducted playbacks for 11 species: 1- Red-breasted Nuthatch (*Sitta canadensis*), 2- Brown Creeper (*Certhia americana*), 3- Hairy Woodpecker (*Picoides villosus*), 4- Yellow-bellied Sapsucker (*Sphyrapicus varius*), 5- Northern Flicker (*Colaptes auratus*), 6- Downy Woodpecker (*Picoides pubescens*), 7- Three-toed Woodpecker (*Picoides tridactylus*), 8- Black-backed Woodpecker (*Picoides arcticus*), 9- Pileated Woodpecker (*Dryocopus pileatus*), 10- Swainson's Thrush (*Catharus ustulatus*), 11- Boreal Chickadee (*Poecile hudsonicus*). Song playbacks were played after each point count. For each species, a sound recording of calls, songs and/or drumming were played at each visit during a one-minute period followed by a 30 seconds interval. Each detection of the focal species was noted, as for the point counts, in two distance classes (< 75 or > 75 m). To avoid calling individuals that were outside the patch, the volume of the recording was adjusted to be human-audible at 75 m from the speaker. Playback data was

compiled by year specifying the occurrence of each species at each station. If a species was detected during point counts, the occurrence was noted in the playback data.

1.3.4 Landscape context

The landscape context was assessed using digital forest cover maps around each sampling station at three different scales: local (radius of 75 m) and landscape (500 m and 1-km). These maps describe each homogenous area at a minimum scale of one to eight hectares, depending on the land use (ex.: unproductive forest or productive forest). We consider that 500 m and one-kilometer radius (314 ha) are large enough areas to describe the effects of the landscape context on forest birds that usually have a territory of few hectares (Askins *et al.* 1987, Drapeau *et al.* 2000, Bowman 2003). Landscape characteristics were calculated by using the mean characteristics of all forested stands, weighted by their area. In order to describe the level of fragmentation of mature forest habitat in the landscape, the proportion of young (< 7 m), intermediate (7-12 m), mature forests (> 12 m) and coniferous mature forests (> 12 m with > 50 % of conifers) were also calculated. The overall proportion of forest (from recent cutblocks to old forests) in the landscape was also considered.

1.3.5 Local habitat

Even though the selection of forest remnants was conducted to minimize differences in forest cover, we conducted at each point count station vegetation inventories to statistically control for the variability of local habitat conditions. Live and dead standing trees were sampled from the center of variable-radius plots by using a wedge prism (basal area factor 2) (Mitchell 1995, Mitchell *et al.* 2001, Potvin and Bertrand 2004). This method determines the total density of trees (trees/hectares) and their density for several diameter classes (10-20, 20-30 and > 30 cm DBH) (Mitchell 1995). We used Imbeau and Desrochers' (2002) tree decay classification chart to characterize the degradation stage of standing trees, but we modified it into four groups: A- healthy trees (classes 1 and 2), B- unhealthy trees (class 3), C- complete snags (classes 4 and 5) and D- incomplete snags (classes 6-8) (Figure 1.2). The density of trees for each of these classes was calculated. In addition, the vertical structure was taken at the center of each point count and at four plots located at 50 m in each cardinal direction from the center. Vegetation structure was estimated for three vegetation layers:

overstory (> 12 m), understory (7-12 m) and shrub layer (< 7 m). For each layer, the percentage of vegetation cover and the proportion of conifers in the cover were taken (Drapeau *et al.* 2000, Lichstein *et al.* 2002, Venier and Pearce 2005). Canopy closure was also noted. Vegetation structure was summarized for each layer for each station (the mean cover of the 5 plots). Moreover, spatial heterogeneity of the conifer cover was characterized for each layer using the Sörensen coefficient of similarity (Legendre 1998, Drapeau *et al.* 2000).

1.3.6 Annual variation of bird communities

Principal components analysis was used to describe the variation in bird communities at the station's scale (Legendre 1998, Drapeau *et al.* 2000). It permitted us to compare the stations by using the individual species abundance between the three years. Prior to the analysis, the species data were Hellinger-transformed. This transformation is appropriate for ordination of species abundances (Legendre and Gallagher 2001, Hirst and Jackson 2007). Standard deviation ellipses (1-sd) were overlaid to represent the differences between the sampling years. All the statistical analysis analyses were done using the R software (R Development Core Team, 2010).

1.3.7 Measuring the contribution of local vs landscape variables in bird community structure

Canonical analyses are frequently used for analysis of bird communities (Drapeau *et al.* 2000, Schieck and Hobson 2000, Holmes and Pitt 2007). They permit a reduction in the number of dimensions of the data, thus allowing the relationship between the species and the environment, but also the species/species interactions to be summarized (Legendre 1998, Peres-Neto *et al.* 2005, Hirst and Jackson 2007). The analysis was made using the bird abundance data from the three inventory years. The 2006 sampling protocol (2x20 min. visits) was slightly different than the two other years (3x15 min.). We consider that this difference should not affect the results because the total sampling effort was comparable (40 min. vs 45 min.), which should provided a detailed characterization of the bird assemblages at the level of individual sampling station (Drapeau *et al.* 1999).

Prior analysis showed slightly significant yearly variation in the avian community composition (R^2=0.058, p=0.005). Yearly fluctuations were removed by detrending the bird abundance by year, using multiple regressions. Detrended data correspond to regression residuals (Legendre 1998). In order to obtain an appropriate representation of the species data, data were also transformed using the Hellinger transformation (Legendre and Gallagher 2001). The use of the detrended data in further analysis allows us to analyze the data from the three years together.

All chosen environmental variables were known to possibly influence bird populations (Bibby and Burgess 2000). Thus, all the landscape variables used in this study were considered because they were all related to our main biological hypothesis, the landscape fragmentation of mature forest cover. Principal components analysis (PCA) of the sampling stations by the environmental variables was applied to each descriptor group (local, 500 m and 1-km) in order to summarize the main biophysical gradients (Legendre and Anderson 1999, Brotons *et al.* 2003, Guénette and Villard 2005). This ordination also eliminated the collinearity among the explanatory variables. Descriptors were properly transformed to reduce their asymmetry. Each predictor group was scaled (ordination of the correlations) and the eigenvectors were conserved for further analyses (Legendre 1998).

In landscape studies, spatial autocorrelation can be a concern because of the proximity of sampling units, resulting in a lack of independence between stations (Fortin and Dale 2005). In our study, the point count stations were at a minimum distance of 200 m. The landscape was characterized within a radius up to 1-kilometer. Several sampling stations had overlapping landscapes at the 1 km scale. Knowing the territoriality of most forest birds, the occurrence of an individual at one station may affect the probability of occurrence at adjacent stations. Therefore, the sampling stations were not entirely independent because of spatial autocorrelation in the explicative and the response variables. In the case of statistical testing, this could be a problem because it affects the confidence interval of the coefficients (Legendre 1998, Fortin and Dale 2005). The spatial structure was modeled using principal coordinates of neighbourg matrices (PCNM). These are obtained by the eigenvalue decomposition of a truncated distance matrix. This approach permits us to model the spatial pattern over multiple scales by using only the points' coordinates. It is then possible to use the PCNM vectors as covariates in partial canonical analyses or regressions (Borcard and

Legendre 2002, Griffith and Peres-Neto 2008). Point counts spaced by more than two kilometers were considered to be spatially independent groups. This extent was chosen to eliminate any overlap in landscape variables (1-km radius). PCNMs were then calculated separately for stations belonging to each independent group. This method was used because PCNMs can only be computed with a good coverage of the sampling region (Borcard and Legendre 2002, Griffith and Peres-Neto 2008), which was not the case with our sampling design.

To examine which scale (local or landscape) had the greatest influence on bird communities, a variation partitioning approach was used (Drapeau *et al.* 2000, Borcard and Legendre 2002, Heikkinen *et al.* 2004). This method permits the calculation of the amount of variation inside the species dataset (Hellinger-transformed detrended abundance data) for different scales: local, 500 m and 1-km, while controlling for spatial autocorrelation (PCNM) (Borcard *et al.* 1992, Peres-Neto *et al.* 2006). During this analysis, all the principal components corresponding to each scale were used. Peres-Neto et al. (2006) demonstrated that the adjusted canonical R-square statistics are more accurate when all the variables are used. Because the relation between bird abundance and their environment may not be linear (Guénette and Villard 2005, Betts *et al.* 2007), multivariate regression trees were used to describe the variation in bird communities in accordance with the local and landscape variables (De'ath 2002). We first detrended the Hellinger-transformed abundance data with the year and the PCNMs to control for the spatial autocorrelation.

The influence of landscape variables on bird communities was tested by partial RDA with permutations while controlling for local variables and spatial autocorrelation. Statistical testing was done by permutations of the residuals (9 999 permutations). This analysis permitted us to examine the significance and the strength of the relationships between the landscape and forest bird communities.

This methodology was used to analyze the point counts abundance data corresponding to each species and to each habitat-specific guild as well. Species were grouped in accordance to the classification by Drapeau *et al.* (2000) with the following categories: A- early successional habitat, B- young forest, C- mature forest, D- forest generalist and E- generalist. The occurrence of the focal species sampled with song playbacks was also analyzed using the same approach.

1.4 Results

1.4.1 Local and landscape characteristics

At the local scale, our sampling stations were primarily dominated by black spruce (*Picea mariana*), balsam fir (*Abies balsamea)* and jack pine (*Pinus banksiana*). White-birch (*Betula papyrifera*) and poplar (*Populus tremuloides*) were also present. The stations had a mean tree density of 246 stems per hectare and were largely dominated by conifer stems with a diameter between 10 and 20 cm (mean 168 trees/ha). Mean snag density was 141 stem/ha. Stations were mostly characterized by an open coniferous canopy (< 20 % of closure) and a closed shrub layer (a mean closure of 75 %) (table 1.1).

The landscape analysis revealed a wide range of mature and old forest cover surrounding the stations (table 1.2). Landscapes within a 1-km radius of sampling stations varied from a dominance of young forests that cover up to 59 % of the landscape, to mature forest landscapes (up to 78 % of the landscape). Therefore, the studied stations were embedded in landscape contexts that differed broadly by the age of the forest cover (23-78 years old), their canopy density (18-64%) and their height (6-17 m).

A deeper analysis of stations' landscape contexts at larger scales (up to 10 km radius) showed that the amount of mature conifer forest (> 12 m) globally decreased as the study scale increased, following a reciprocal relation, which stabilized at approximately 12 % of the landscape (figure 1.3). Alternatively, the amount of young forest (< 7 m) increased as the scale increased, up to 25% of the landscape. However, regardless of the extent of landscape context analysis, the amount of forests higher than 7 meters (other than coniferous mature forest) stabilized close to 40 %. Percent cover of the different forest cover types across our study region stabilized at a radius between one and two kilometers.

1.4.2 Bird communities

1.4.2.1 Overall patterns

Throughout the three sampling years, 73 different species were detected at the point count stations inside the 75 m radius (see table 1.3 for species list). Most of them were species associated with mature forest (40 %). The mean species occurrence was 12 species

per station. Eight bird species, including five species associated with mature forests (Golden-crowned kinglet, Nashville Warbler, Yellow-rumped Warbler, Magnolia Warbler and Ruby-crowned Kinglet), were detected in 50 % of the point counts (figure 1.4). Hence, forest-dwelling birds mostly dominated the bird community of these stations. The majority of the species did not exhibit large yearly variation in occurrence or abundance (figure 1.4 and 1.5). The abundance of the different habitat-specific guilds did not vary with the amount of coniferous mature forest remaining in the landscape (table 1.4). Interestingly, more birds associated with mature forests were detected in highly fragmented landscapes (< 15 % of mature forest in a radius of 1-km) than in less fragmented landscapes (> 45 %). (table 1.4).

1.4.2.2 Yearly variations

The principal component analysis of bird community composition for our 72 sampling stations explained 19 % of the variation with the first two axes (figure 1.6). The high overlap in the ellipses, which depicts bird community composition and structure from different sampled years, suggests slight yearly variations but also consistent community structure over the three years.

1.4.2.3 Relative contribution of local and landscape contexts in bird communities

The partitioning of the variation in the species abundance matrix was determined with regards to the explanatory power of the local and landscape variables while considering the spatial autocorrelation of the sampling sites (24 orthogonal PCNM vectors). The global adjusted R-square, describing the relationships between the abundance and explanatory variables at the three scales (local, 500 m and 1-km), was 19.6 %. Of this value, local habitat characteristics accounted for 16.46 % of the variation. The two landscape scales explained only 2.5 % of the variation that was not explained by the local variables (table 1.6). Even if the landscape's variance was significant ($p < 0.001$), the amount of explained variance was quite low. The regression tree analysis led to the same conclusion with only 3.3 % of the sites correctly classified. It identified only one threshold indicating different community structures between stations that have more of less than 63 % of conifer cover in the overstory (> 12 m) at the local scale. Interestingly, the communities of the stations that have a coniferous overstory (> 63 % of conifers) are still dominated by species associated with mature forests, but with abundances lower than less coniferous stations (table 1.5).

Similar results were obtained with the analysis of the habitat-specific guilds (global adjusted R^2= 20.6%), where local conditions explained 16.3 % of the variation and the landscape alone, only 4 % (p = 0.014) (table 1.6). The variation in the playback data was also partitioned in the same manner. The global adjusted R-square was 0.16. The local conditions and the landscape alone explained almost the same amount of variation (respectively 4.8 % and 3.4 %). A relatively high amount of the variation is shared between both scales (6 %). The adjusted R-square relative to the spatial component (PCNMs) was higher in the analysis of the guilds (adj R^2 = 3 %) and of the playback data (adj R^2 = 4 %) in comparison to the community study analysis (adj R^2 = 0.02) (table 1.6). Hence, there is more autocorrelation in these datasets than in the other.

1.5 Discussion

1.5.3 Matrix permeability for mature forest birds in managed forest landscapes

In a review paper on the effect of habitat loss and fragmentation on songbird communities in landscapes managed for timber harvesting, Schmiegelow and Mönkönnen (2002) concluded that fragmentation effects including edge effects (biological and physical), area effects and isolation effects were generally weak when compared to findings in agro-forested landscapes (Whitcomb *et al.* 1981b, Ambuel and Temple 1983, Robbins *et al.* 1989, Robinson *et al.* 1995, Donovan *et al.* 1997, Bender *et al.* 1998, Villard *et al.* 1999). They argue that contrary to agro-forested ecosystems, landscapes under timber management do not undergo land use conversion that leads to a binary classification of landscape in forest/non-forest habitat. Hence, landscapes remain forested but the texture (*sensu* Wiens 1994) of the matrix changes. In boreal forests such changes usually correspond to a shift in the age structure of the forest mosaic where early regenerating and young forest stages become dominant compared to the expanse of old forest cover types given that fire cycles are longer than even-aged rotations (Drapeau *et al.* 2000, Bergeron *et al.* 2002, Bergeron *et al.* 2007).

While landscapes managed for timber production have considerably reduced amounts of old forest cover, the resulting landscape mosaic of different forest cover types may be more permeable to forest birds movements than in agro-forested landscapes where boundaries between habitat types are sharp and forest patches are often embedded in a

matrix that is hostile (*sensu* Askins 1995). Hence, the reluctance of forest birds to cross recent cutblock areas (Desrochers and Hannon 1997, Rail et al. 1997, Bélisle and Desrochers 2002, Bélisle and St. Clair 2002, Gobeil and Villard 2002) may be temporary in managed landscapes. Regenerating areas and young forest habitats may be used by forest birds (Imbeau *et al.* 1999, Norton *et al.* 2000, Robichaud *et al.* 2002). Young forests could be more important habitats than first thought either through facilitating dispersal mechanisms of mature forest birds across the landscape or by providing marginal breeding habitats or both. Future research could thus investigate the different functions (movements, foraging areas or nesting habitats) of young forests for mature forest birds.

In our study, the regional landscape (4 000 km^2) contained a large amount young forest cover types (7-12 m in height) that covered up to 43 % of the land base. The importance of young forest cover at the regional scale could explain the persistence of mature forest birds in our forest remnants, and this even though our design covered a wide gradient of habitat loss of mature forest at landscapes scales that are usually recognized important for forest birds (McGarigal and McComb 1995, Drolet *et al.* 1999, Drapeau *et al.* 2000, Betts *et al.* 2007). Likewise, our results may also be suggestive of the more general trends of weak response of songbirds to mature forest fragmentation effects such as size effects, isolation effects or edge effects in timber managed landscapes (Schmiegelow and Mönkkönen 2002, Batáry and Báldi 2004). The regional importance of young forest habitats and the fact that such cover types cannot be considered non-habitat for forest songbirds should be considered in future analyses of habitat fragmentation effects on songbirds in timber managed landscapes.

Our results indicate that the composition of bird communities in mature forest remnants was not strongly affected by the contrasting matrices (clearcuts, young forest cover and mature forest cover measured at the neighbouring landscape scale (500 m and 1000 m radii) given the small amount of explained variation measured in our models. The regression tree analysis reveals that the bird community composition of remnants stations embedded into young deciduous landscapes was however quite similar to the one of remnants in older mature landscape. Moreover, at the level of individual species/habitat relationships we did not find strong non-linearity or thresholds.

1.5.4 Long-term persistence of songbirds

Detection of species occurrence and abundance in a given habitat do not necessarily mean that they are able to reproduce (Van Horne 1983, Vickery *et al.* 1992, Purcell and Verner 1998). Some remnants might act as 'sources', which would permit the colonization of forest habitats that are transitions from young to mature forests (Brown and Kodric-Brown 1977). In this case, a rescue effect may permit communities of birds associated with mature forests to be sustained in remnants, even if mature and older forest cover types do not dominate the landscape. Some remnants may not, however, be sustainable habitats for forest-dwelling birds. Several studies in remnants of agro-forested landscapes have found some evidence of source-sink dynamics among birds populations (Donovan *et al.* 1995, Brawn and Robinson 1996, Porneluzi and Faaborg 1999, Burke and Nol 2000, Bayne and Hobson 2001, Dufault 2007). Better assessment of breeding activity and reproductive success of songbirds in remnant habitats of timber harvested landscapes should be a logical next step for assessing if these remnants can be considered quality habitats for the maintenance of forest songbirds in timber managed landscapes

1.6 Conclusion

The tolerance and persistence of mature forest associates of songbird communities in remnant mature forests could be an indication of the resilience of songbirds to large-scale disturbances in boreal landscapes. In these, the frequency and size of natural disturbances such as wildfires have created landscape mosaics of various forest cover types under which songbirds have evolved (Monkkonen and Welsh 1994, Niemi *et al.* 1998, Schmiegelow and Mönkkönen 2002). However, the percent cover of old forest under current even-aged management is below historical levels (Lesieur *et al.* 2002, Cyr *et al.* 2009). Hence, the persistence of mature forest species in remnant patches could at least in part be tied to the nature of the matrix in which they are embedded, particularly with regards to the functional role of the quantity of young forests (7-12 m). For certain guilds such as open cup nesters - foliage gleaners, these younger forest stands could be secondary habitats that may be suitable for breeding. Species relying on senescent trees and decaying wood such as woodpeckers may, however, not find suitable nesting conditions, but nevertheless disperse through these habitats. For these old forest specialists preserving mature forest in managed forests is critical. Future studies on the occupancy and reproductive activity of songbirds are

required to better assess the contribution of young forests in their overall demography in forest landscapes managed for timber production.

1.7 References

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1.8 Figures

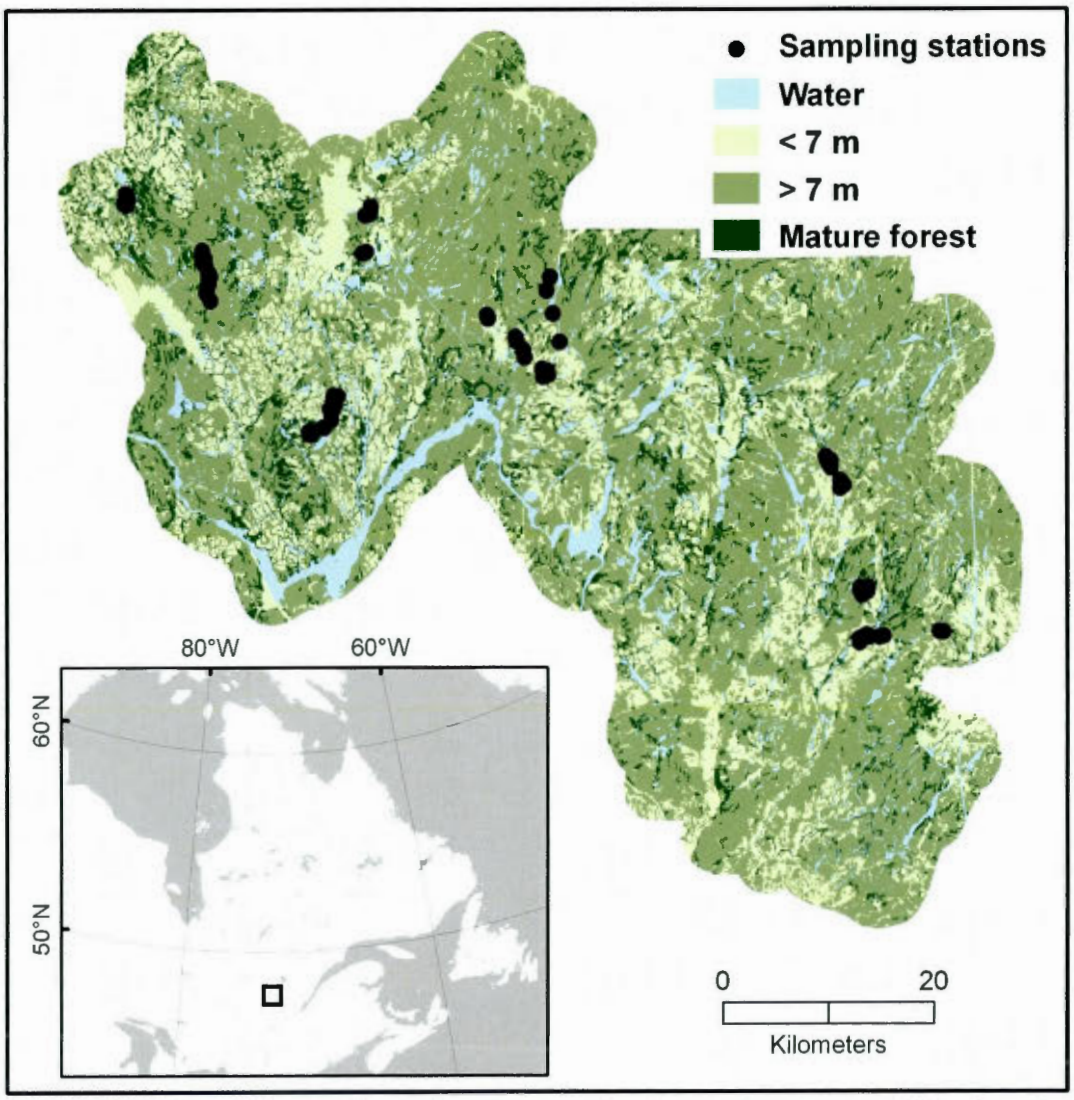

Figure 1.1: Map of the study region showing the forest structure and the location of the sampling stations.

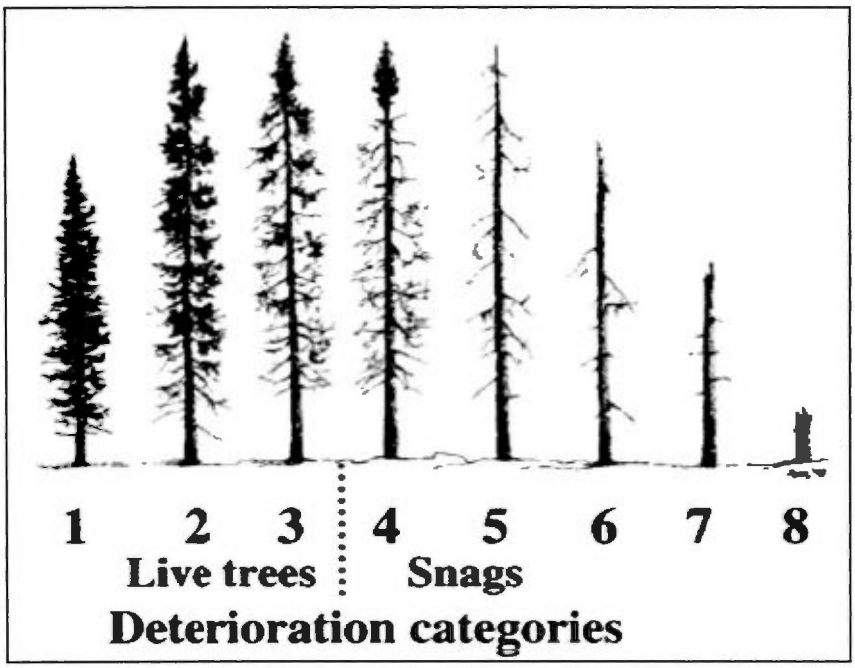

Figure 1.2: Tree decay classification chart from Imbeau and Desrochers (2002).

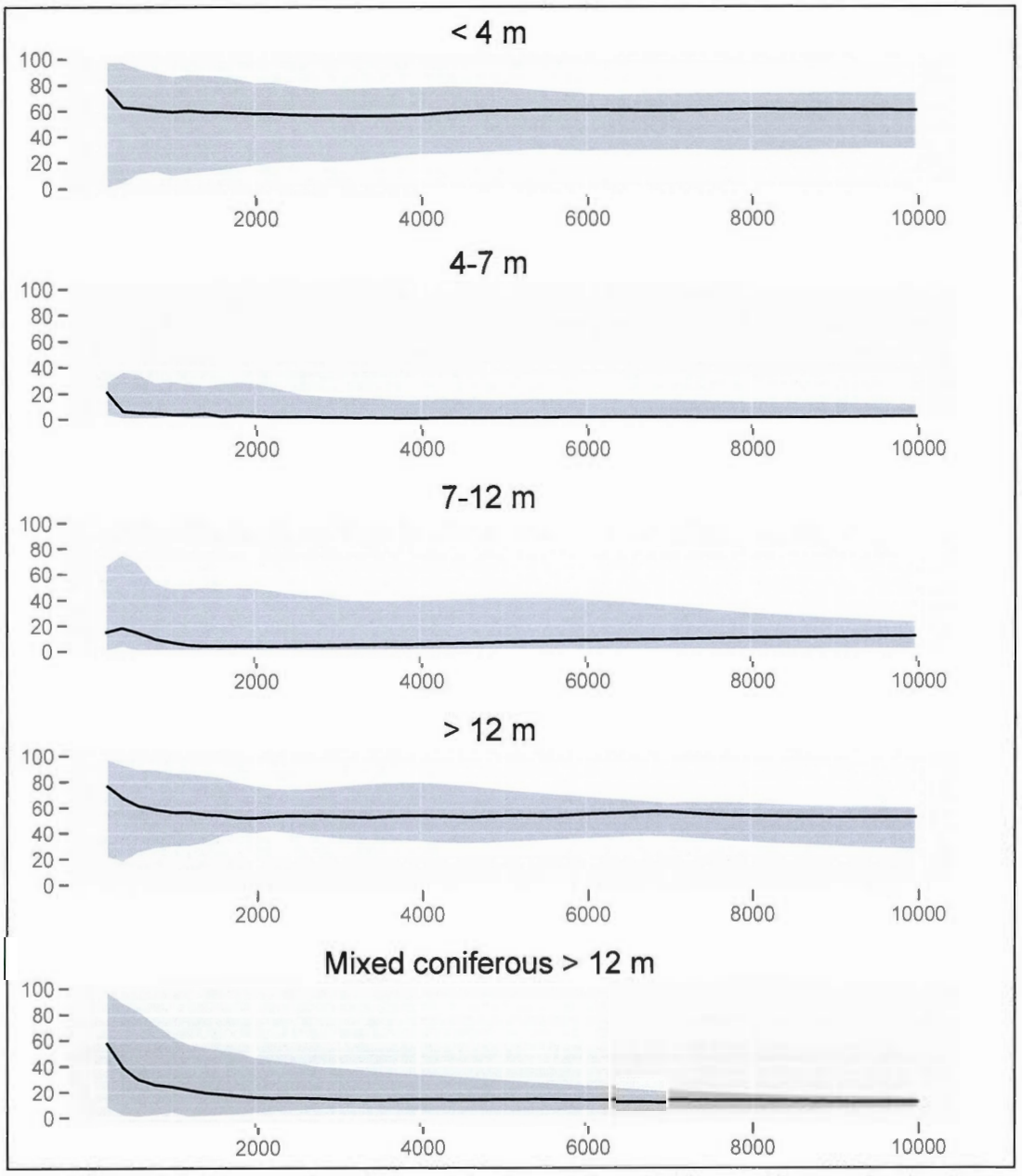

Figure 1.3: Proportion of forest (< 4 m, 4-7 m, 7-12 m, >12 m and mixed coniferous forest > 12 m) at different radii (100-10 000 m) around sampling stations. For each, the median and the range of variability are shown.

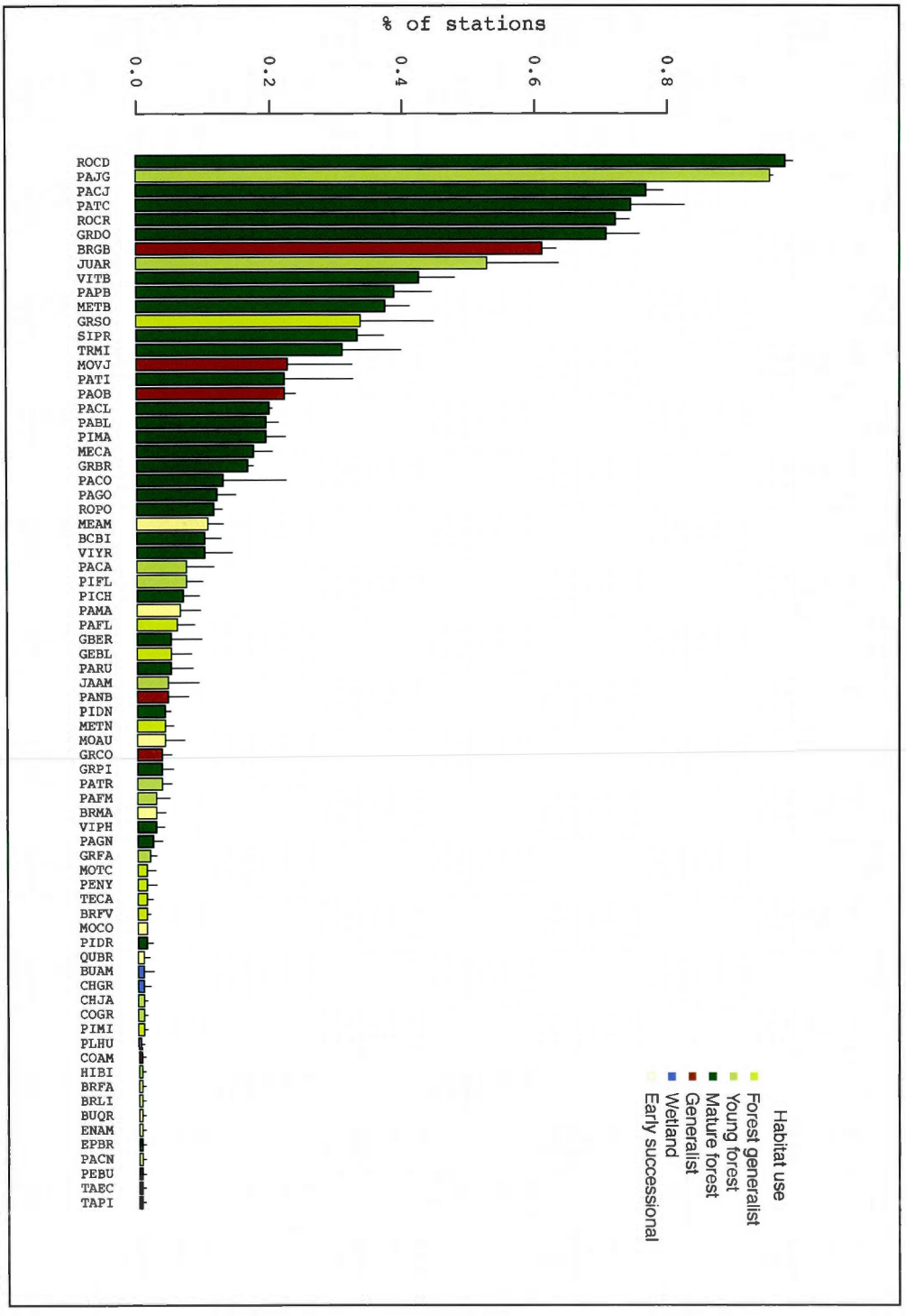

Figure 1.4: Rank-occurrence plot. Yearly mean proportion of stations where each species was detected (± standard error). See table 1.3 for definition of the abbreviations.

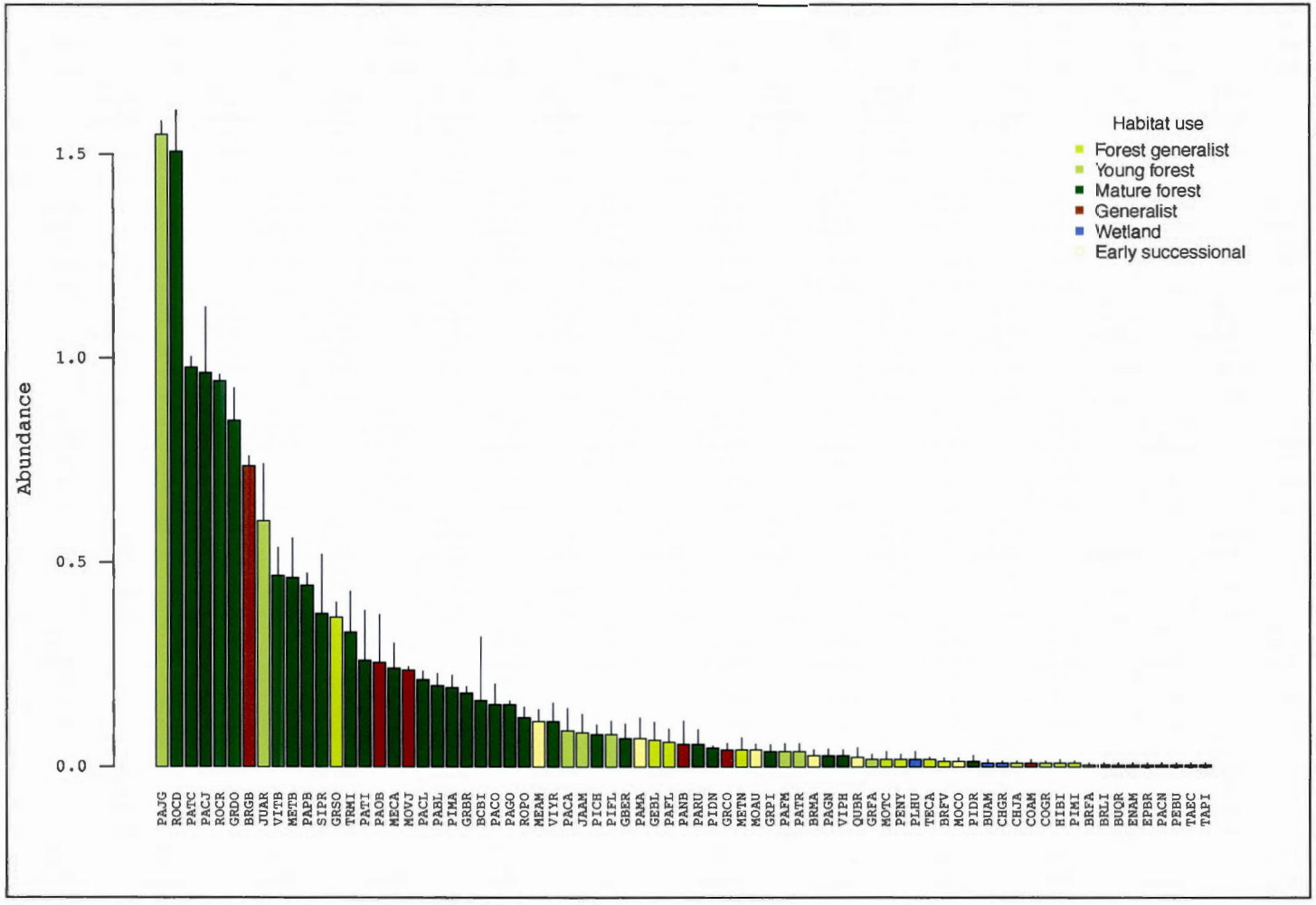

Figure 1.5: Rank-abundance plot. Mean annual bird species abundance at each station with standard error. See table 1.3 for definition of the abbreviations.

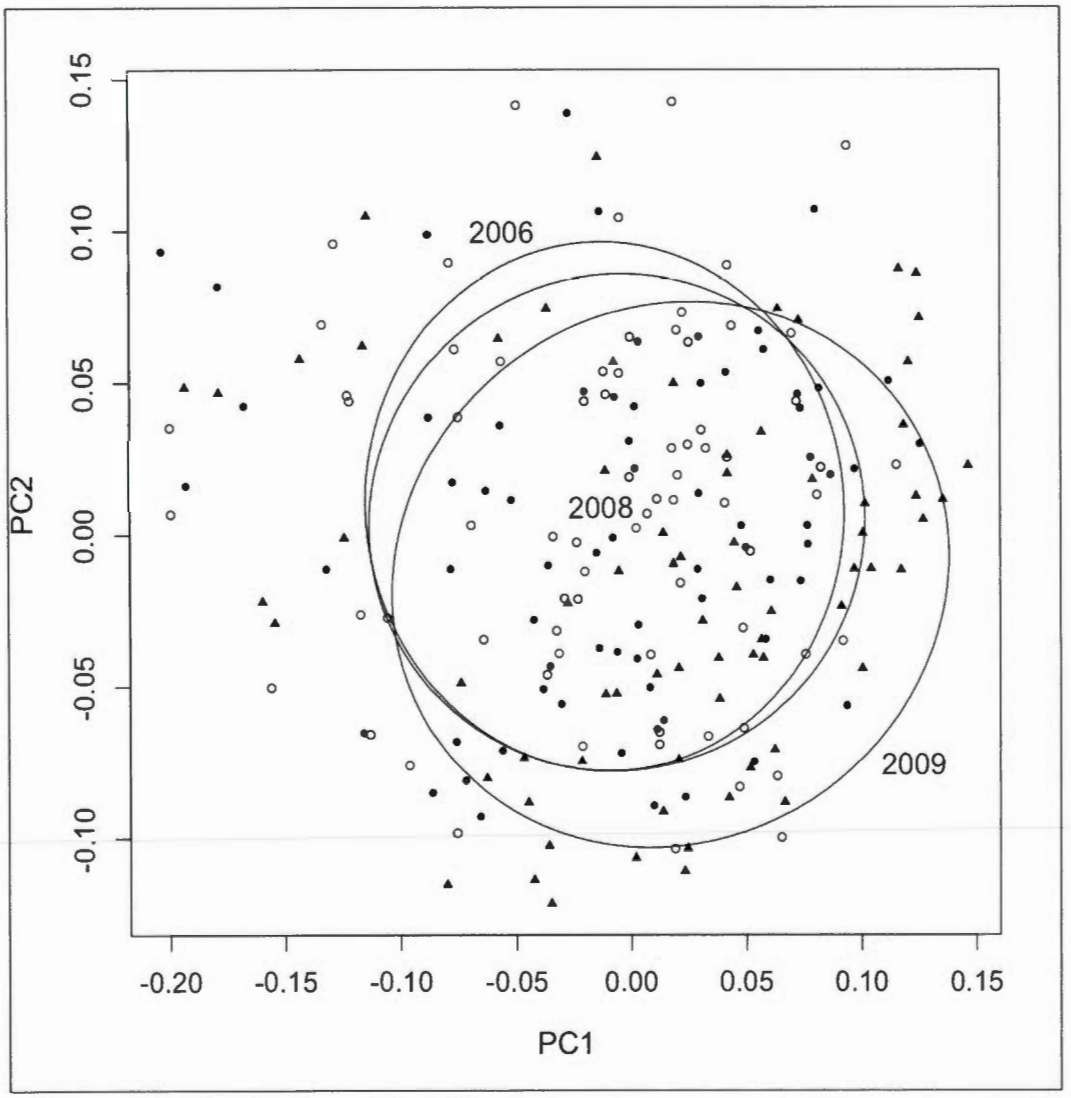

Figure 1.6: Ordination of the 72 point counts representing the three years of data. The distance biplot was obtained by a principal component analysis of the individual species abundance at the stations. The ellipses (one standard deviation) represent the three sampling years. The first axis represent 12% of the variation of the species data; the second, 7%.
Legend: ○ : 2006, ● : 2008 and ▲ : 2009

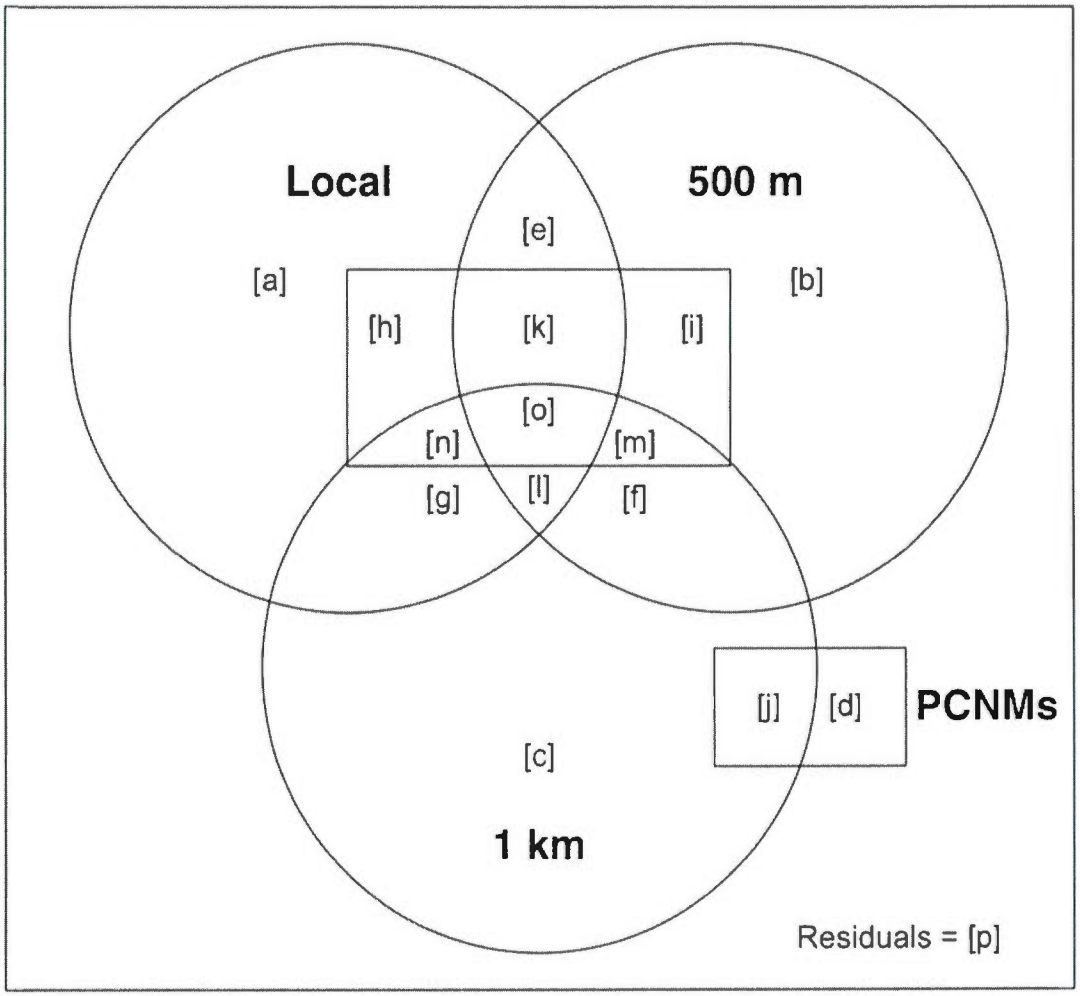

Figure 1.7: Part definitions of variation partitioning analysis with four groups of explanatory variables: three scales (local, 500 m and 1-km radii) and the PCNMs for the spatial autocorrelation. The parts [a,b,c] represent the variation that is only associated with the local, 500 m and 1-km scales respectively. Overlapping sections represent the part of the variation that is shared between different groups of variables.

1.9 Tables

Table 1.1: Station habitat characteristics of the stations

	Median	Range
Stem density (10-20 cm) (stem/ha)	162	(0-558)
Stem density (>20 cm) (stem/ha)	58	(0-181)
Conifer density (10-20 cm) (stem/ha)	146	(0-492)
Conifer density (> 20 cm) (stem/ha)	52	(0-171)
Stem density (stem/ha)	239	(36-636)
Conifer density (stem/ha)	221	(31-539)
Snag density (10-20 cm) (stem/ha)	90	(0-420)
Snag density (>20 cm) (stem/ha)	20	(0-190)
Conifer snag density (10-20 cm) (stem/ha)	55	(0-420)
Conifer snag density (> 20 cm) (stem/ha)	10	(0-190)
Snag density (stem/ha)	120	(0-580)
Conifer snag density (stem/ha)	70	(0-520)
Overstory cover (> 12 m)	16%	(4-52)
Understory cover (7-12 m)	38%	(10-68)
Shrub layer cover (< 4 m)	52%	(8-78)
Overstory proportion of conifers	88%	(32-88)
Understory proportion of conifers	88%	(52-88)
Shrub layer proportion of conifers	78%	(32-88)

Table 1.2: Characteristics of the landscape around the sampling station at three radii (75 m, 500 m and 1-km), calculated from digital forest cover maps

	75 m		500 m		1 km	
	median	range	median	range	median	range
Coniferous cover	87%	(45-88)	62%	(31-88)	58%	(30-81)
Canopy density	51%	(43-70)	49%	(16-69)	45%	(18-64)
Tree height	14 m	(10-20)	13 m	(6-18)	12 m	(6-17)
Proportion of forest	100%	(93-100)	92%	(59-100)	93%	(80-98)
Proportion of young forest (< 7 m)	0%	(0-14)	11%	(0-65)	23%	(0-59)
Proportion of intermediate forest (7-12 m)	0%	(0-100)	0%	(0-75)	2%	(0-50)
Proportion of mature coniferous forest	96%	(0-100)	31%	(0-90)	24%	(0-65)
Proportion of mature forest	99%	(0-100)	54%	(1-94)	47%	(5-78)
Age	70 yrs	(46-90)	55 yrs	(22-88)	50 yrs	(23-78)

Table 1.3: Species detected inside the point counts

Common name	Scientific name	CODE	Habitat use†
White-winged Crossbill	*Loxia leucoptera*	BCBI	MAF
Chipping Sparrow	*Spizella passerina*	BRFA	SHR
Fox Sparrow	*Passerella iliaca*	BRFV	FGEN
White-throated Sparrow	*Zonotrichia albicollis*	BRGB	GEN
Lincoln's Sparrow	*Melospiza lincolnii*	BRLI	SHR
Swamp Sparrow	*Melospiza georgiana*	BRMA	SHR
American Bittern	*Botaurus lentiginosus*	BUAM	WET
Red-tailed Hawk	*Buteo jamaicensis*	BUQR	SHR
Spotted Sandpiper	*Actitis macularia*	CHGR	WET
American Goldfinch	*Carduelis tristis*	CHJA	YOF
American Crow	*Corvus brachyrhynchos*	COAM	GEN
Ruby-throated Hummingbird	*Archilocus colubris*	COGR	YOF
Common Nighthawk	*Chordeiles minor*	ENAM	SHR
Sharp-shinned Hawk	*Accipiter striatus*	EPBR	MAF
Evening Grosbeak	*Coccothraustes vespertinus*	GBER	MAF
Blue Jay	*Cyanocitta cristata*	GEBL	FGEN
Brown Creeper	*Certhia americana*	GRBR	MAF
Common Raven	*Corvus corax*	GRCO	GEN
Swainson's Thrush	*Catharus ustulatus*	GRDO	MAF
Veery	*Catharus fuscescens*	GRFA	YOF
Pileated Woodpecker	*Dryocopus pileatus*	GRPI	MAF
Hermit Thrush	*Catharus guttatus*	GRSO	FGEN
Tree Swallow	*Tachycineta bicolor*	HIBI	YOF
Cedar Waxwing	*Bombycilla cedrorum*	JAAM	YOF
Dark-eyed Junco	*Junco hyemalis*	JUAR	YOF
American Robin	*Turdus migratorius*	MEAM	SHR
Gray Jay	*Perisoreus canadensis*	MECA	MAF
Boreal Chickadee	*Poecile hudsonicus*	METB	MAF
Black-capped Chickadee	*Parus atricapillus*	METN	FGEN
Alder Flycatcher	*Empidonax alnorus*	MOAU	SHR
Olive-sided Flycatcher	*Contopus borealis*	MOCO	SHR
Least Flycatcher	*Empidonax minimus*	MOTC	FGEN
Yellow-bellied Flycatcher	*Empidonax flaviventris*	MOVJ	GEN
Black-throated Blue Warbler	*Dendroica caerulescens*	PABL	MAF
Canada Warbler	*Wilsonia canadensis*	PACA	YOF
Yellow-rumped Warbler	*Dendroica coronata*	PACJ	MAF
Northern Parula	*Parula americana*	PACL	MAF
Wilson's Warbler	*Wilsonia pusilla*	PACN	SHR
Ovenbird	*Seiurus aurocapillus*	PACO	MAF
American Redstart	*Setophaga ruticilla*	PAFL	FGEN

Table 1.3 : Species detected inside the point counts (continuation)

Common name	Scientific name	CODE	Habitat use†
Chestnut-sided Warbler	*Dendroica pensylvanica*	PAFM	YOF
Black-throated Green Warbler	*Dendroica virens*	PAGN	MAF
Blackburnian Warbler	*Dendroica fusca*	PAGO	MAF
Nashville Warbler	*Vermivora ruficapilla*	PAJG	YOF
Common Yellowthroat	*Geothlypis trichas*	PAMA	SHR
Black-and-white Warbler	*Mniotilta varia*	PANB	GEN
Tennessee Warbler	*Vermivora peregrina*	PAOB	GEN
Bay-breasted Warbler	*Dendroica castanea*	PAPB	MAF
Northern Waterthrush	*Seiurus noveboracensis*	PARU	MAF
Magnolia Warbler	*Dendroica magnolia*	PATC	MAF
Cape May Warbler	*Dendroica tigrina*	PATI	MAF
Mourning Warbler	*Geothlypis philadelphia*	PATR	YOF
Broad-winged Hawk	*Buteo platypterus*	PEBU	MAF
Northern Saw-whet Owl	*Aegolius acadicus*	PENY	FGEN
Hairy Woodpecker	*Picoides villosus*	PICH	MAF
Black-backed Woodpecker	*Picoides arcticus*	PIDN	MAF
Three-toed Woodpecker	*Picoides dorsalis*	PIDR	MAF
Northern Flicker	*Colaptes auratus*	PIFL	YOF
Yellow-bellied Sapsucker	*Sphyrapicus varius*	PIMA	MAF
Downy Woodpecker	*Picoides pubescens*	PIMI	FGEN
Common Loon/Great Northern Diver	*Gavia immer*	PLHU	WET
Common Grackle	*Quiscalus quiscula*	QUBR	SHR
Golden-crowned Kinglet	*Regulus satrapa*	ROCD	MAF
Ruby-crowned Kinglet	*Regulus calendula*	ROCR	MAF
Purple Finch	*Carpodacus purpureus*	ROPO	MAF
Red-breasted Nuthatch	*Sitta canadensis*	SIPR	MAF
Scarlet Tanager	*Piranga olivacea*	TAEC	MAF
Pine Siskin	*Carduelis pinus*	TAPI	GEN
Spruce Grouse	*Falcipennis canadensis*	TECA	FGEN
Winter Wren	*Troglodytes troglodytes*	TRMI	MAF
Philadelphia Vireo	*Vireo philadelphicus*	VIPH	MAF
Blue-headed Vireo	*Vireo solitarius*	VITB	MAF
Red-eyed Vireo	*Vireo olivaceus*	VIYR	MAF

† Habitat use classification from Drapeau et al. (2000)

Table 1.4: Mean number of detections per station for each habitat-specific guild according to the amount of coniferous mature forest remaining in the landscape (1-km) and their standard error

% coniferous mature forest	Early successional	Young forest	Mature forest	Forest generalist	Generalist	Wetland
< 15% (n=48)	0.50 ± 0.02	2.60 ± 0.02	9.88 ± 0.06	0.73 ± 0.02	1.00 ± 0.02	0.10 ± 0.02
15-30% (n=114)	0.28 ± 0.01	2.61 ± 0.01	10.39 ± 0.03	0.61 ± 0.01	1.57 ± 0.01	0.02 ± 0.00
30-45% (n=39)	0.26 ± 0.01	2.36 ± 0.03	8.31 ± 0.08	0.44 ± 0.02	1.21 ± 0.02	0.03 ± 0.00
> 65% (n=15)	0.07 ± 0.02	2.00 ± 0.07	7.13 ± 0.15	0.73 ± 0.05	1.00 ± 0.06	0.00 ± 0.00

Table 1.5: Mean number of detections per station for each habitat-specific guild according to the amount of conifers in the overstory at the local scale and their standard error. The threshold was obtained by the multivariate regression tree analysis of the individual species abundance table.

	% of conifer canopy cover	
	<63% (n=195)	>63% (n=21)
Early successional	0.19 ± 0.02	0.32 ± 0.00
Young forest	2.05 ± 0.08	2.57 ± 0.01
Mature forest	13.1 ± 0.17	9.30 ± 0.02
Forest generalist	0.86 ± 0.05	0.58 ± 0.00
Generalist	1.10 ± 0.06	1.36 ± 0.01
Wetland	0.05 ± 0.01	0.04 ± 0.00

Table 1.6: Variation partitioning of the species abundance matrix (communities), habitat-specific guilds abundance and occurrence focal species (playbacks). Only the positive adjusted R-squares are presented, since negatives R-squares occur because of collinearity between the groups of explanatory variables (Peres-Neto *et al.* 2006). See figure 1.7 for the interpretation of the fractions.

Fractions	Adjusted R-squares		
	communities	habitat guilds	playbacks
[a]	0.083	0.107	0.039
[b]	0.006	0.023	0.019
[c]	0.007	0.025	0.012
[d]	0.002	0.006	0.033
[e]	0.012	0.010	0.002
[f]	0.010	0.001	
[g]	0.008		0.004
[h]			
[i]	0.003	0.002	0.001
[j]	0.008	0.002	0.002
[k]	0.001	0.008	0.003
[l]	0.051	0.054	0.052
[m]			
[n]		0.008	
[o]	0.017	0.017	0.021
[p] = Residuals	0.804	0.778	0.839
TOTAL (adj R^2)	0.196	0.222	0.161

CHAPITRE II

BREEDING ACTIVITY OF A MATURE FOREST BIRD SPECIES IN FOREST REMNANTS IN A HIGHLY FRAGMENTED BOREAL MIXED CONIFER-HARDWOOD FOREST

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2.1 Abstract

Effects of habitat loss and fragmentation of mature forest on songbirds' reproductive activity in forest remnants have been highly documented in forest lands altered by agriculture or urban expansion. Less knowledge is however available on reproductive activity of birds in remnant habitats created by timber harvesting. This study documents the reproductive activity of mature forest associate, the Golden-crowned Kinglet (*Regulus satrapa*), in remnant habitats of a managed conifer-hardwood mixedwood boreal forest in Quebec. We tested the hypothesis that this species will have lower reproductive success in remnants embedded in fragmented landscapes than in an unfragmented landscape. Fourteen remnant stands, ranging in size from 10 to 17 hectares, characterized by mature forest cover and embedded in landscapes (radius of 1 km) of different ages (30-85 years-old) were sampled in 2009. Territory mapping and intensive monitoring of family groups permitted us to follow the status of 59 territorial males while measuring their pairing and subsequent reproductive success. Of the mapped territories, 52 were occupied by a breeding couple and 46 led to juvenile-fledging success. We analyzed the effects of local habitat conditions and landscape scale characteristics on 1) the density of territorial males per remnant, 2) the pairing success and 3) the reproductive success in these kinglet territories. We found that breeding kinglets are more influenced by local characteristics of their habitat than by landscape variables. Moreover, these results suggest micro-habitat selection at the territory scale. The reproductive success of this species remained high (78 % success) in all remnant habitats despite the isolation resulting from harvesting of the forest matrix in the surrounding landscape. Our results indicate that this species is tolerant to forest disturbances at the landscape scale for both density and reproductive success of territorial males. We suggest that managed forest landscapes might constitute non-hostile environments for forest-dwelling birds like kinglets because they usually contain a high amount of young forest at the regional scale instead of non-forest habitat, thus dampening the effects of mature habitat loss and fragmentation.

Keywords: Golden-crowned Kinglets, *Regulus satrapa*, reproduction, managed landscape, forest remnants, habitat loss, fragmentation, boreal forest, fledging success, pairing success

2.2 Introduction

Industrial timber harvesting has become the major disturbance in many regions of the boreal forest (Belleau *et al.* 2007, Drapeau *et al.* 2009). It has transformed the landscape mosaic from a dominated mature and older forest system to an early-seral stage matrix (Bergeron and Harvey 1997, Bergeron *et al.* 2001). The loss of mature and late-seral forests negatively affects songbird communities associated with these habitats, resulting in a change in species assemblages at the landscape scale (McGarigal and McComb 1995, Schmiegelow *et al.* 1997, Drapeau *et al.* 2000). Recent studies have mostly documented the prevalence of habitat loss and less, the role of fragmentation in forest systems managed for timber production (Andrén 1995, Hobson and Bayne 2000, Schmiegelow and Mönkkönen 2002). While the composition of bird communities is strongly tied to characteristics of the habitat at the local scale (Pearson 1993, Bibby and Burgess 2000, Hobson *et al.* 2000, Lichstein *et al.* 2002), several studies in forests managed for timber production have shown that the occurrence and abundance of songbird populations living in remnant forests can be affected by timber harvesting at the landscape scale (Hagan *et al.* 1997, Drapeau *et al.* 2000, Penhollow and Stauffer 2000). Furthermore, the resulting remnants can be affected by edge effects (Bayne and Hobson 1997, Kurki *et al.* 1997). There is a lack of knowledge about the carrying capacity of the managed mosaic to maintain biodiversity (Bergeron *et al.* 2007). While studies have shown that songbirds are significantly influenced by the landscape composition or patch conditions (Schmiegelow *et al.* 1997, Drapeau *et al.* 2000), the ability of these remnants to support reproductive activity with regards to their landscape context has been far less documented (but see Bayne and Hobson 2001).

Remnants of mature forests in harvested landscapes are often left in cutover areas either because of legislation or due to inaccessibility (ex: steep slopes, wet areas, etc.). Assessing whether birds successfully breed in these stands is a better indicator of habitat quality than quantifying their occurrence or abundance (Van Horne 1983, Vickery *et al.* 1992, Purcell and Verner 1998). Predation and parasitism, for example, are known to affect the reproductive success of birds in agro-forested remnants (Bayne and Hobson 1997, Burke and Nol 1998, Burke and Nol 2000, Bayne and Hobson 2001, Bayne and Hobson 2002, Schmiegelow and Mönkkönen 2002, Batáry and Báldi 2004). The number of individuals detected in forest fragments can thus be a misleading indicator of their ability to persist in

these forests (Pulliam 1988, Donovan *et al.* 1995, Brawn and Robinson 1996, Porneluzi and Faaborg 1999, Burke and Nol 2000). Forested landscapes managed for timber harvesting do not have the same properties as agro-forested landscapes. A forested landscape is always evolving or recovering towards forest. Forest disturbances promote the creation of temporary habitats in opposition to the sharp and permanent edges of agro-forested landscapes. Hence, some evidence suggests that fragmentation in landscapes managed for timber harvesting may not affect bird reproductive success or nest predation rates as strongly as in agro-forested landscapes (Andrén 1995, Cotterill and Hannon 1999, Manolis *et al.* 2002, Schmiegelow and Mönkkönen 2002, Boulet *et al.* 2003, Batáry and Báldi 2004). It is possible that the amount of young forest cover in managed landscapes may generate regional forest conditions that facilitate movements for mature forest birds, thus mitigating the effects of mature habitat loss and fragmentation (see Chapter I). For example, songbirds usually associated with mature forests can use early-seral stages to disperse (Imbeau *et al.* 1999, Robichaud *et al.* 2002, St-Laurent *et al.* 2008). Therefore, the connectivity between forest patches may explain the persistence of some species in small forest fragments (Robbins *et al.* 1989).

The main objective of this study was to document the effects of habitat loss and fragmentation on a forest-dwelling bird that lives in forest remnants, the Golden-crowned Kinglet (*Regulus satrapa*). In the present study, we chose this species because it is an insectivorous short-distance migrant known to live in mature coniferous forests and to be very sensitive to habitat loss and alteration (Guénette and Villard 2005, Venier and Pearce 2005, Stuart-Smith *et al.* 2006, St-Laurent *et al.* 2008). It is also susceptible to be affected by landscape scale disturbances (Drapeau et al. 2000). We predict that the density of territorial males of mature forest remnants in managed landscapes should be inferior to the density in stands embedded in continuous mature forest. Given that predation levels are not higher in timber managed boreal landscapes (Schmiegelow and Mönkkönen 2002), we predict that pairing success and reproductive success levels of kinglets will be similar to those found in the continuous forest.

2.3 Methods

2.3.1 Study area

This study was conducted in the conifer-hardwood mixed wood boreal forest of the upper part of the Mauricie region, Quebec, Canada (47°53'N, 72°53'W) (figure 2.1). Covering 4 000 km^2, this area is located within the fir and yellow birch bioclimatic domain. The forest cover is mainly dominated by balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) and white spruce (*Picea glauca*) as codominants (Robitaille and Saucier 1998). The landscape is characterized by an undulating topography with 68 % of the study area covered with merchantable timber volumes although some areas are inaccessible for timber harvesting (Levac 2008). Hence, about 10% of the studied region still contains mature mixed-conifer forest.

2.3.2 Study design

In this region, 14 remnant patches (10–17 ha) with similar habitat characteristics were selected using digital forestry maps based on aerial photographs (Quebec Ministry of Natural Resources and Wildlife). GIS analyses were done with ArcGIS (ESRI). By selecting patches with similar habitat conditions, it was possible to test the landscape effect by controlling for local conditions. In the literature, the habitat of the Golden-crowned Kinglet is described to be mostly mature coniferous forest (Galati and Galati 1985, Inglod and Galati 1997, Drapeau *et al.* 2003, Venier and Pearce 2005, Stuart-Smith *et al.* 2006). Therefore, the chosen patches were ≥ 60 years old with at least 50 % of the canopy cover in conifers. Patch heights were > 12 m with > 40 % in closed canopy. Patches were isolated from each other by a minimum distance of one kilometer and were at least 100 m from other mature forests. This distance is recognized by gap-crossing studies as limiting kinglet movements (Desrochers and Hannon 1997, Bélisle and Desrochers 2002).

The landscape context was characterized with digital forest cover maps around the center of the patches within a radius of one kilometer. These maps represent and describe each homogenous area at a minimum scale of one to eight hectares, depending on the land state (ex: unproductive forest or productive forest). We assume that a one-kilometer radius is large enough to describe the effects of the landscape surrounding a kinglets breeding

territory, which covers less than three hectares. The forest conditions neighboring each patch varied from young landscapes, with only 3 % of mature conifer forest to continuous mature forest (47 % mature coniferous forest). The proportion of young forests (< 7 m) in the landscape varied from 0 % to 43 % (table 1.1). To prevent the crowding effect that occurs in recent cutover areas (Hagan and Johnston 1992, Andrén 1994, Schmiegelow *et al.* 1997, Debinski and Holt 2000), the selected patches were not embedded in areas harvested less than five years ago.

2.3.3 Bird monitoring

The Golden-crowned Kinglet is a monogamous species that is highly territorial and that is abundant in late-seral forests of our study region, so it can be easily studied (see Chapter I). We sampled Golden-crowned Kinglet populations, firstly by measuring the density of territorial males (number of territories per hectares) in remnants and finally, by measuring their pairing status and their reproductive success (at least one fledgling juvenile). The use of breeding territory density in whole patches as an indicator of the abundance of bird populations is more precise than relative abundance or presence/absence data (Keller and Anderson 1992, Hagan and Meehan 2002, Betts *et al.* 2007). A spot-mapping methodology (Bibby and Burgess 2000) was used to determine kinglet territory locations in every patch. Between May 22 and June 6 2009, each patch was sampled four times between sunrise and noon. Sampling was done along transects positioned in a manner to standardize the sampling effort (27 minutes/ha/visit). The patch order and transect direction varied at each visit to reduce potential time of day bias on bird's detectability. Censuses were conducted when meteorological conditions were appropriate, i.e., no precipitation and wind speed below 12 km/h. Meteorological conditions can affect birds' behavior and the observer's capacity to detect individuals (Drapeau *et al.* 1999, Bibby and Burgess 2000).

In order to accurately delimit territories, intensive territory mapping was employed. It consists of following each individual to map its movements (Buford *et al.* 1996, Lambert and Hannon 2000). Throughout the breeding season the evolution of each territory was monitored. So, it was possible to gather information about the pairing status of each territorial male and the subsequent reproduction success. A male was considered paired if another individual was within 10 m without exhibiting aggressive behavior or if fledglings were found in its territory. A family group with at least one juvenile, that was able to fly, confirmed fledging

success in a territory. Between June 7 and July 31, up to six visits were made in each territory or until we confirmed fledging success. At each visit, individuals were followed sequentially for 45-60 minutes. In further analyses, only territories with at least 25 % of their area inside the patches were considered. This area is required to permit habitat characterization of a territory. Playbacks of songs and calls were used to confirm the absence of kinglets in areas where they were not detected.

2.3.4 Habitat characterization

Vegetation sampling in fragments allowed us to control *a posteriori* (during statistical analysis), for the slight variability in local habitat conditions. Five vegetation stations, spaced by a minimum distance of 15 m, were randomly located in each territory and 15, in areas outside territories (spaced by 30 m). Live and dead standing trees were sampled from the center of variable-radius plots using a wedge prism (basal area factor 2) (Mitchell 1995). This method evaluates the total density of trees or conifers and their density in different diameter classes (< 10, 10-20, 20-30 and > 30 cm) (Mitchell 1995). To characterize the degradation stage of standing trees we used Imbeau and Desrochers' (2002) tree decay classification, but modified it into four groups: A- healthy trees (classes 1 and 2), B- unhealthy trees (class 3), C- complete snags (classes 4 and 5) and D- incomplete snags (classes 6-8). The density of trees that pertains to each of these classes was calculated. In addition, the vertical structure was measured at the center of the plot for three vegetation layers: overstory (> 12 m), understory (7-12 m) and shrubs layers (< 7 m). For each layer, the percentage of vegetation cover and the proportion of conifers in the cover were estimated. Canopy closure was also noted.

2.3.5 Patch and landscape characterization

Digital forest cover maps are a fast and efficient source of data to coarsely describe patch and landscape characteristics. For the selected patches, maps allowed to complete ground plots information by providing their canopy cover (%), composition (% conifer), area, height and age at a broader scale. At the landscape scale (radii of one kilometer), the same information was obtained by calculating the mean characteristics of all forested stands, weighted by their area. In order to describe the maturity of the landscape, the proportion of young, mature forests and coniferous mature forest was also calculated. Young forests were

considered to be stands < 7 m in height. Mature forests were stands matching the same criterion as the sample patches (see above) but conducted with and without consideration of the stands composition (coniferous or deciduous). In other words, we determined the proportion of mature conifer forests and of all mature forests irrespective of their composition. The overall proportion of forest (from recent cutblocks to old forests) in the landscape was also considered.

2.3.6 Statistical analysis

Exhaustive bird sampling permitted us to delimit all kinglet territories present in the sampled patches. To control for the variable size of the patches, the analyses were conducted using the density of territories (number of territories / ha) as a response variable. One objective of this research was to find the best model of explanatory variables to describe the density of territories. A habitat occupancy model was built using simple linear regressions and descriptors from the local habitat, patch and landscape scales. All statistical analyses were done using R (R Development Core Team 2008).

The number of vegetation sampling stations was not constant between patches because of the unequal number of territories per patch. To avoid unequal sampling, a Jackknife procedure (10 000 runs) was used to calculate the mean characteristics of the local habitat.

A stepwise variable selection procedure was used to select candidate variables from the model with the best goodness of fit. This approach has been criticized because there is a possibility of selecting models that are overfitted or without biological meaning (Burnham and Anderson 2002). In our study, however, all of the chosen environmental variables are known to possibly influence bird populations. There is much information about the relationship between local environmental variables and bird populations, but little is known about the influence of landscape variables. Thus, all the landscape variables used in this study were considered because they are all related to our main biological hypothesis, the effect of landscape maturity. To avoid overfitting the model, it was necessary to reduce the number of variables (Burnham and Anderson 2002). Principal component analysis (PCA) was applied to each descriptor group in order to summarize the main gradients (Legendre 1998, Brotons *et al.* 2003, Guénette and Villard 2005). Ordination also eliminates collinearity among the

explanatory variables. Descriptors were transformed to reduce their asymmetry. Each predictor group was scaled (ordination of the correlations) and the eigenvectors, for which their respective eigenvalues were significant in comparison to the broken stick distribution, were conserved for further analysis (Legendre 1998). Stepwise linear regressions, using Akaike information criterion adjusted for small sample size (AIC_c), were employed to select the model of only two principal components with the best goodness of fit. Because of the limited number of samples, no more than two principal components can be included in the model (Burnham and Anderson 2002). Confidence intervals (95 %) were calculated by bootstrap (10 000 replications). To interpret the principal components, their correlation with original descriptors and the significance of their relationships were computed.

To examine which scale (local or landscape) had the greatest influence on kinglet densities in remnants, a variation partitioning approach was used (Borcard *et al.* 1992, Drapeau *et al.* 2000, Heikkinen *et al.* 2004). This method calculates the amount of variation in the response variable that is explained at different scales (local or 1-km). For each scale, two principal components were selected using stepwise selection.

Modeling of reproduction data was conducted at the scale of kinglet territories, instead of the remnant mature forest patches. Since pairing and reproductive success are binary data, logistic regressions were used with the mean attributes of the local vegetation in the kinglet territories, as well as with the patches and landscape characteristics as explanatory variables. For the same reasons explained before, PCA was used to reduce the dimensionality of the habitat descriptors. Because of the nested nature of the territories within the patches, spatial dependence among the data could pose a problem (Legendre 1998, Fortin and Dale 2005). Autocorrelation among patches was examined within the residual component of the preceding regression (Legendre 1998) using an analysis of variance (ANOVA) to ensure homogeneity.

The sampling scheme allowed us to compare micro-habitats in areas where the kinglets were present vs absent. The mean attributes of the five sampling stations inside each territory were compared to the stations located outside the territories. Classification trees were used to obtain a representation of the thresholds of the relations between environmental variables and kinglet occurrence (Breiman 1984, Feldesman 2002).

2.4 Results

Territory mapping permitted us to delimit a total of 59 territories located within the 14 patches; each one containing from one to eight kinglet territories. The extensive monitoring of family groups allowed us to determine that 52 of the 59 territorial males paired with a female. Furthermore, at least one fledgling was produced in 46 of the 59 territories.

2.4.1 Local habitat

In total, 505 vegetation stations were visited in order to characterize vegetation in the remnants. The remnants were primarily dominated by black spruce (*Picea mariana*), balsam fir with white birch as codominant. Yellow-birch (*Betula alleghaniensis*), poplar (*Populus tremuloides*), red maple (*Acer rubrum*) and jack pine (*Pinus banksiana*) were also present. Remnants generally had a coniferous (~75 % conifers) canopy for which the overstory (> 12 m) was open (~20 % vegetation cover), and the understory (7-12 m) was closed (65 %). (table 2.2). The stations located outside kinglet territories (n = 295) were slightly different than the ones located inside kinglet territories (n = 210). They had a greater deciduous cover (28 %) and the overstory was 50 % more closed.

2.4.2 Density of territories

The principal component analysis of the local habitat-related variables yielded three axes explaining 76 % of the global variance (table 2.3). The patch and landscape PCA summarized respectively 78 % and 80 % of the variance, each with only two axes. The model selection method identified two principal components (axes 1 and 3) that best described kinglet territory density. Both components selected belonged to the set of local habitat variables. Other possible models were not as plausible as the one chosen, since their AIC_c were at least two points higher than the one selected (Burnham and Anderson 2002).

The first selected axis was significantly related to a closed coniferous forest with a high stem density and with canopy opening (table 2.3). It was also negatively correlated with the density of large trees (DBH > 30 cm). The second selected axis was related to the quantity of standing snags and to the proportion of coniferous cover in the understory and in the canopy. The regression model containing both of these components explained over half

the variation in the data ($p < 0.001$, $R2 = 0.517$)(table 2.4). Both axes were positively and significantly correlated with the density of kinglet territories in a patch (table 2.3).

The variance partitioning approach identified 24 % of the variation that was imputable to the local habitat scale. The landscape context did not have any additional effect (0 %). Therefore, it can be argued that kinglets choose mature remnants in which to establish their territories for their inherent characteristics and that the adjacent environment did not seem to have a significant influence.

2.4.3 Reproductive success of territorial males

The fledging success analysis was done at the scale of the territories. Preliminary analysis revealed three territories that were outliers in terms of habitat characteristics, so the analyses were conducted using 55 territories instead of the 59. PCA permitted us to reduce the dimensionality of the three variable groups. Two axes were conserved for the patch and landscape scales and five, for the local habitat. For each group, the selected axes represented approximately 75 % of the intra-group variance. The logistic regression model with all of the components had a Nagelkerke pseudo-R^2 of 0.211. None of the components were significantly related to reproductive success ($p > 0.05$)(table 2.5). The spatial dependence of territories was tested and was not significant ($p = 0.74$). Removing outliers did not affect the results. Almost all territorial males were paired with a female (88 %). Hence, pairing success was high throughout our sample set.

2.4.4 Micro-habitats within the territories

The classification tree analysis describing the micro-selection of kinglet habitats inside patches revealed that the kinglets seem to establish their territories in the most coniferous parts of the remnants (misclassification rate of 17 %). The territories (34 %) were in areas where the sub-canopy (4-12 m) and the shrub layer (< 4 m) were mostly closed by conifers (respectively, > 33 % and 60-75 % of closure), with less than 40 % of the sub-canopy in deciduous cover (figure 2.2).

2.5 Discussion

It is surprising that landscape characteristics did not have a significant influence either on the densities of kinglet territories or on their reproduction. Other studies have determined that below a certain proportion of suitable habitat in the landscape (< 9-30 % depending on the species), the abundance of some species that live in remnants may be affected (Andrén 1994, Fahrig 1997, Betts *et al.* 2010). The majority of our mature coniferous forest remnants, which were embedded in a regional matrix of less than 12 % of the landscape in mature forest cover, would thus have been expected to have lower densities of kinglet territories or reduced mating and reproductive success and this was not the case. In managed temperate deciduous forests, Betts et al. (2007) did, however, find a threshold of habitat amount at which the populations of Golden-crowned Kinglet responded. They tested several scales (150-2000 m radii), but only the smallest one (150 m) was significant with a threshold at 50 % of habitat at the local scale. In another study, Allard et al. (Chapter I) showed that songbird communities, including kinglet populations in mature remnants did not seem to be affected by the level of mature forest fragmentation and habitat lost at landscape scales of 500 m and 1-km). These results, at the bird assemblage level, point in the same direction as the current study for a mature forest-dwelling specialist, the Golden-crowned Kinglet. In other words, loss and fragmentation of mature forest cover within landscapes of 500 and 1000 m radii do not seem to affect kinglet territory densities or the species' reproductive activity. Instead, kinglets occupy most mature remnants but concentrate their territories within portions where the quality of available habitats is high (density of conifers in the understory) at a local scale.

In the literature, this species is known to nest in mature forests dominated by a dense coniferous cover (Galati and Galati 1985, Inglod and Galati 1997, Drapeau *et al.* 2003, Venier and Pearce 2005, Stuart-Smith *et al.* 2006). Both density and cover of conifers were determinant factors in the habitat selection process of kinglets at the scale of individual territories. Hence, our fragments provided high quality habitat for kinglets that resulted in pairing and reproductive success comparable to those found in continuous forests. Interestingly, our analysis showed a negative relationship between kinglet territories and percent of overstory closure. This is because overstory trees that were responsible for overstory closure were intolerant deciduous species (trembling aspen and white birch) that

are not used for nesting by kinglets. The shape of deciduous tree crowns provides a greater closure of the canopy than do conifers (Farrar 1995). Our results suggest the absence of a patch size effect on the density of kinglet territories and on their subsequent reproduction, in remnants larger than 10 ha. In this study, the remnants had an area between 10-17 ha with a minimum width of about 120 m. This is consistent with other studies that found that 60 m wide strips have similar kinglet density as continuous forests (Darveau *et al.* 1995, Leboeuf 2004, Potvin and Bertrand 2004).

In our study, sampling effort was considerable in order to obtain data on the number of succesful territories (i.e., that produced at least one fledgling). It is possible that some fledglings were not detected in a few territories. In this case, the observed reproductive success (78 %) should be considered a minimum. Nonetheless, even though our study was conducted in forested landscapes modified by industrial forest activities, our results were similar to those from continuous unmanaged forests. For example, the fledging success obtained by Galati and Galati (1985) in a continuous mature forest environment was 80 %. It can thus be argued with such data on reproductive activity and success that the mature forest remnants of this study provided suitable nesting habitats for the kinglet population.

In agricultural landscapes the ability of small remnants to sustain populations has been questioned due to increased predation and/or parasitism (Andrén 1995, Robinson *et al.* 1995, Donovan *et al.* 1997, Thompson III *et al.* 2000, Boulet *et al.* 2003). This system seems to be mainly affected by predator communities (top-down regulation). However, the increase in predation levels is not clear in the boreal forest (Schmiegelow and Mönkkönen 2002). Although we didn't directly study predation, the high reproductive success of kinglets in our study, suggests that increased predation may not be an issue. Moreover, food resources do not seem be a factor limiting populations of insectivorous birds in fragmented landscapes (bottom-up dynamic), because forests seem to have higher arthropod densities near edges and in small fragments (Whitaker *et al.* 2000, Harris and Reed 2002).

Animal species can select their habitat at different scales. They respond to habitat configuration at a large scale but may choose their breeding territory based on fine-grained features at the local scale (Morrison *et al.* 1992). In our study, the regional landscape is not mainly composed of coniferous mature forests, yet it contains a large amount (70 % of the studied region) of forest > 7 m in height. Whereas the harvested forest matrix is hostile to

forest-dwelling bird movements immediately following harvesting (Desrochers and Hannon 1997, Rail *et al.* 1997, Bélisle and St. Clair 2002), many species, like the Golden-crowned Kinglets, seem to start reusing these habitats when the forest reaches the sapling stage (2-7 m) (Imbeau *et al.* 1999, Norton *et al.* 2000, Robichaud *et al.* 2002, St-Laurent *et al.* 2008). Hence, these habitats, even if not optimal, represent a non-hostile environment for forest-dwelling birds. At the kilometer scale, some stations were surrounded by up to 43 % of the landscape in young forests (< 7 m). It is thus surprising that these stations harbour kinglet populations similar to continuous mature forest. The reason may be that the landscape conditions nearby forest remnants are more heterogeneous at a small scale than at a regional scale. The high loss of mature forest habitat within one-kilometer around the sampling stations may be damped by the high amount of non-hostile forest habitat (forest cover of > 7 m) at the regional scale. Boreal forest birds may be adapted to variable forest conditions because of the natural disturbance regime of the boreal forest, which leads to a boreal forest landscape that is always evolving. Habitat flexibility and tolerance of forest-dwelling birds with regards to these different forest cover types would thus explain in part their persistence in boreal forest remnants in a managed landscape. These factors may explain the difference between the findings of studies on the strong relationships between avifauna and landscape composition or configuration variables in agro-forested landscapes and the weak relationships found in forests managed for timber production, particularly in boreal ecosystems (Schmiegelow and Mönkkönen 2002). Since this study doesn't allow testing these hypotheses directly, further research is required to investigate the use of intermediate forests (> 7 m) by mature forest-dwelling birds.

Our results suggest that remnants of mature forests may be quality habitats for birds associated with mature forest provided that the managed matrix does not impede movements of species. Golden-crowned Kinglets do not seem to be affected by fragmentation and loss of mature conifer forests in our study area, this in a region where the history of timber harvesting has transformed the forest mosaic for more than a century. Although it has been discussed that effects of habitat loss and fragmentation of older forest on organisms may be dampened by the transient nature of the matrix (clearcuts regenerating into forests; see Schmiegelow and Mönkkönen 2002), our results pinpoint the importance of young forest cover (7-12 m in height) as a key matrix attribute for the persistence of mature forest associates in older forest remnants. Whereas such habitat may not be optimal it nevertheless may not be hostile to

forest-dwelling birds' movements. While forest managers should maintain older forest cover in managed landscapes as refuge habitats for reconstructing mature songbird populations, more attention should be devoted to landscape planning of the managed matrix. The amount and spatial configuration of young forest cover may prove to be a key element to long-term persistence of forest-dwelling species in older forest remnants.

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2.7 Figures

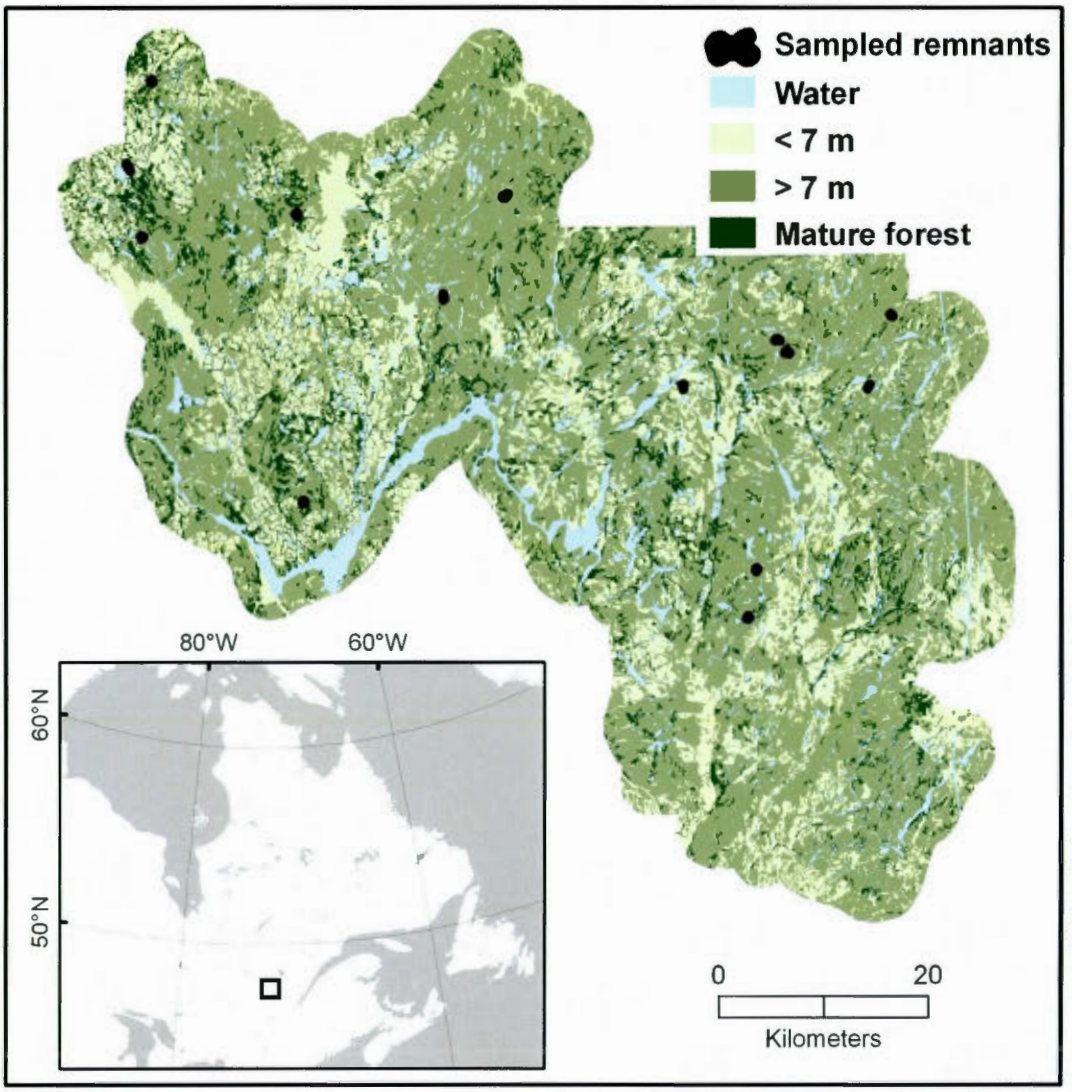

Figure 2.1: Map of the study region showing the forest structure and the location of the sampled remnants.

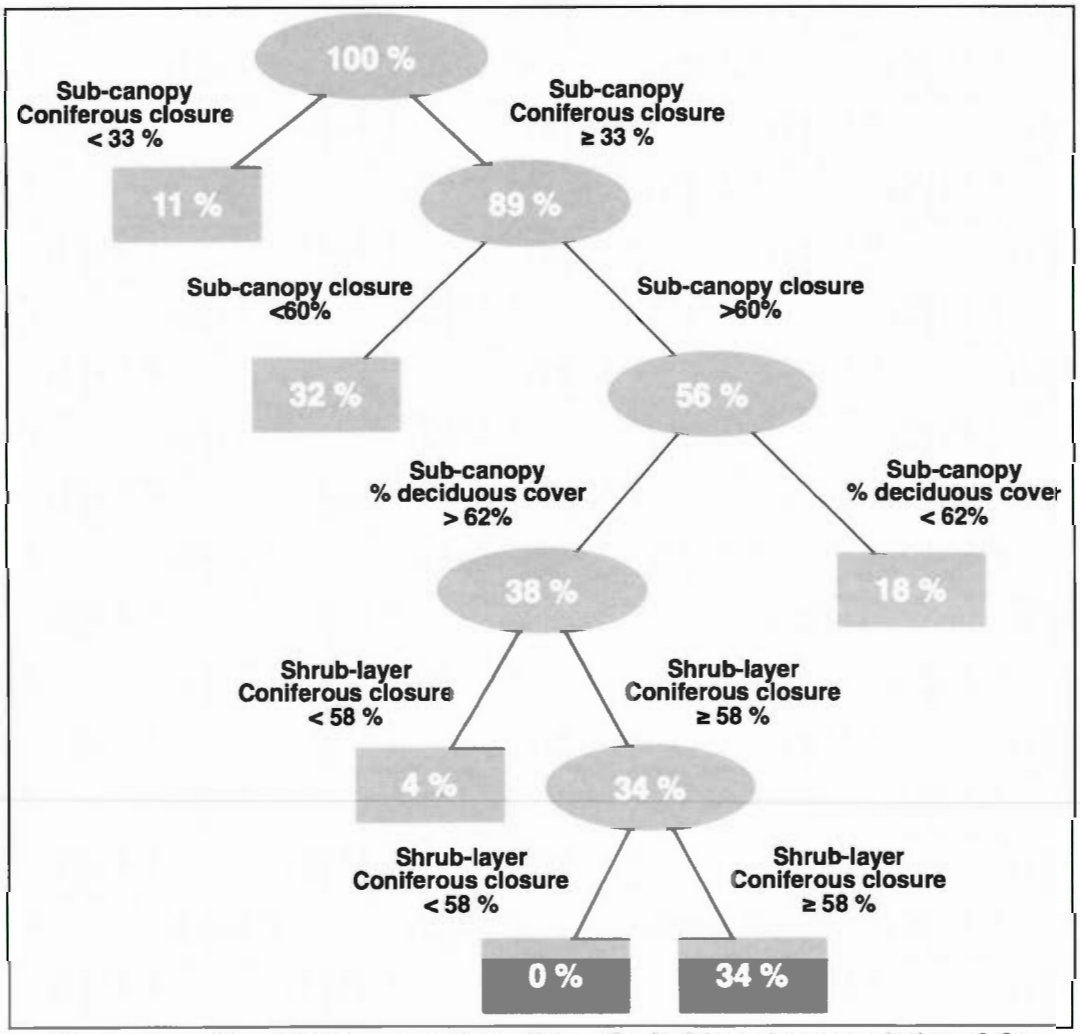

Figure 2.2: Classification tree describing the habitat characteristics of the kinglet's territories (n=44) by using a binomial classification. The proportions of territories that correspond to the two choices are indicated in the boxes.

Table 2.1: Characteristics of the remnants and their landscape within a 1-km radius, calculated from digital forest cover maps

	Patch		1 km	
	median	range	median	range
Resinous cover	67%	(50-88)	58%	(36-84)
Canopy density	56%	(50-75)	55%	(43-78)
Tree height	16	(14-20)	13	(9-16)
Age	84	(70-100)	55	(31-86)
Proportion of forest			89%	(59-98)
Proportion of young forest (< 7 m)			6%	(0-43)
Proportion of intermediate forest (> 7 m)			25%	(0-60)
Proportion of mature resinous forest			16%	(3-47)
Proportion of mature forest			34%	(13-92)

Table 2.2: Mean habitat characteristics inside and outside the territories with their standard error

	In		Out	
	mean	SE	mean	SE
Stem density (0-10 cm) (stem/ha)	863	67	1018	109
Stem density (10-20 cm) (stem/ha)	221	7	181	9
Stem density (20-30 cm) (stem/ha)	52	2	40	2
Stem density (>30 cm) (stem/ha)	8	1	13	1
Conifer density (0-10 cm) (stem/ha)	617	56	606	87
Conifer density (10-20 cm) (stem/ha)	176	7	137	9
Conifer density (20-30 cm) (stem/ha)	42	2	28	2
Conifer density (>30 cm) (stem/ha)	6	0	6	1
Total stem density (stem/ha)	1145	67	1251	108
Total conifer density (stem/ha)	841	57	777	88
Overstory cover	16%	1	24%	2
Understory cover	65%	1	59%	2
Shrublayer cover	71%	1	71%	2
Overstory proportion of conifers	78%	1	60%	2
Understory proportion of conifers	72%	1	61%	2
Shrublayer proportion of conifers	69%	1	57%	2

Table 2.3: Correlation of the habitat variables with the significant principal components

	PC1	PC2	PC3
Stem density (0-10 cm) (stem/ha)	0.408	-0.708	0.065
Stem density (10-20 cm) (stem/ha)	0.809	0.329	0.278
Stem density (20-30 cm) (stem/ha)	0.048	0.800	0.445
Stem density (>30 cm) (stem/ha)	-0.921	-0.177	0.141
Conifer density (0-10 cm) (stem/ha)	0.778	-0.571	0.008
Conifer density (10-20 cm) (stem/ha)	0.955	0.143	0.075
Conifer density (20-30 cm) (stem/ha)	0.536	0.662	0.250
Conifer density (>30 cm) (stem/ha)	-0.570	-0.244	0.272
Total stem density (stem/ha)	0.475	-0.658	0.117
Total conifer density (stem/ha)	0.838	-0.494	0.032
Overstory cover	-0.567	0.204	0.659
Understory cover	-0.465	-0.427	0.661
Shrublayer cover	-0.460	-0.556	0.215
Overstory proportion of conifers	0.903	0.018	-0.071
Understory proportion of conifers	0.938	0.124	-0.062
Shrublayer proportion of conifers	0.849	-0.276	-0.129
Total explained variance	0.404	0.221	0.133

Table 2.4: Linear regression coefficients of the analysis of kinglet density in remnants

	Values	SE	Confident intervals (95%)	p.values
Intercept	0.3407	0.0282	(0.286 - 0.400)	<0.001
PC1	0.0305	0.0096	(0.052 - 0.012)	0.009
PC3	0.0401	0.0167	(0.005 - 0.074)	0.035

Table 2.5: Linear regression coefficients of the analysis of kinglet reproduction of remnants

	Estimate	Standard error	z value	p.value
Intercept	1.534	0.400	3.832	<0.001
local.PC1	-0.017	0.229	-0.073	0.942
local.PC2	-0.242	0.245	-0.990	0.322
local.PC3	-0.416	0.295	-1.412	0.158
local.PC4	0.398	0.263	1.512	0.131
local.PC5	0.554	0.318	1.745	0.081
patche.PC1	-0.503	0.480	-1.048	0.295
patche.PC2	0.450	0.408	1.104	0.270
landscape.PC1	-0.033	0.210	-0.159	0.874
landscape.PC2	0.080	0.268	0.298	0.766

CONCLUSION GENERALE

Le rôle des jeunes forêts du paysage

En milieu forestier, les travaux réalisés ces dernières années sur les communautés d'oiseaux des peuplements résiduels de forêts aménagées pour la coupe n'ont pas montré d'effets significatifs de la configuration (taille, isolement et effets de lisières) du paysage adjacent et cela, même s'ils se trouvent dans des environnements peu propices aux oiseaux associés aux forêts matures (Schmiegelow et Mönkkönen 2002). Compte tenu de l'historique de perturbations de la région étudiée, où le couvert régional en forêt mature n'est plus que de 10 %, et de la grande variabilité de maturité des paysages étudiés (1-km de rayon), nous considérions que cette région offrait des conditions propices à un appauvrissement en espèces associées aux forêts matures des communautés d'oiseaux, de même qu'à un succès d'appariement et de reproduction plus faible des oiseaux de forêts matures dans les forêts résiduelles. Il est donc étonnant de ne pas avoir trouvé de telles relations entre les caractéristiques et le niveau de maturité du paysage et la structure des communautés d'oiseaux ou le statut de reproduction d'une espèce associée aux forêts matures. Il est d'autant plus notable que ce résultat ne semble pas varier beaucoup entre les trois années d'échantillonnage. On peut en conclure que dans notre région d'étude, les effets de la perte d'habitat et de la fragmentation n'affectent pas de manière significative la structure des communautés et la reproduction d'espèces de forêts matures. Les peuplements résiduels de paysages fortement fragmentés et jeunes avaient des communautés semblables à celles de paysages matures, tout en permettant la reproduction d'une espèce associée aux forêts matures. Nos résultats viennent appuyer l'idée que la réponse des oiseaux à la perte d'habitat et à la fragmentation des forêts bien documentée dans les milieux agroforestiers n'est pas directement applicable aux oiseaux en forêts aménagées à des fins de production ligneuse. (Andrén 1994, Mönkkönen et Reunanen 1999, Lichstein *et al.* 2002, Schmiegelow et Mönkkönen 2002). Notre étude se démarque de ces autres études par le fait que nous écartons l'hypothèse qu'à une échelle régionale le couvert forestier mature vienne atténuer les effets observés à l'échelle du paysage (500 m et 1-km). En effet, notre protocole

expérimental a délibérément été établi pour contrôler cet effet en réalisant l'étude dans une région qui en raison de sa longue historique de coupe (plus de 100 ans) a réduit le couvert forestier mature à des proportions en deçà des seuils d'habitat critiques (10 – 30 %) reconnus dans la littérature (Andrén 1994, Betts *et al.* 2007).

D'autre part, bien que les oiseaux forestiers aient des affinités d'habitat et que certains soient considérés comme des spécialistes des forêts matures et âgées, plusieurs études ont montré une certaine flexibilité dans les caractéristiques des habitats qu'ils peuvent utiliser (Imbeau *et al.* 1999, Robichaud *et al.* 2002, St-Laurent *et al.* 2008). Ainsi, les oiseaux forestiers peuvent se retrouver dans des habitats suboptimaux qui leur permettraient de répondre à certains de leurs besoins, tels leur dispersion ou encore comme habitat temporaire. Il devient alors difficile de conceptualiser les effets de la perte et la fragmentation de l'habitat dans les forêts aménagées comme c'est le cas dans les milieux agroforestiers qui considèrent la matrice comme habitat/non-habitat (McGarigal et McComb 1995, Drapeau *et al.* 2000, Lichstein *et al.* 2002). La capacité d'une jeune matrice forestière à supporter des populations d'oiseaux associées aux forêts matures et à permettre leur reproduction est encore méconnue. Nos résultats indiquent qu'il est important d'approfondir nos connaissances sur leurs différents rôles dans le maintien des communautés associées aux forêts matures.

L'importance de l'échelle d'étude

Il est difficile de définir les échelles d'étude auxquelles les oiseaux forestiers peuvent être influencés (Wiens 1995). Il est acquis que les oiseaux possèdent des affinités avec leur environnement immédiat, leur habitat local, car celui-ci doit être capable de subvenir entre autres à leurs besoins d'espaces et d'alimentation (Morrison *et al.* 1992, Bibby et Burgess 2000). D'ailleurs, notre étude indique que les oiseaux forestiers utilisent leur habitat davantage en fonction des caractéristiques locales des peuplements résiduels qu'en fonction de la matrice adjacente. De plus, il semble qu'en milieu agroforestier les oiseaux peuvent être affectés à de petites échelles, par exemple par un effet de bordure accru qui semble diminuer la productivité des espèces associées aux forêts matures (Gibbs et Faaborg 1990, Porneluzi *et al.* 1993, Villard *et al.* 1993, Andrén 1995, Robinson *et al.* 1995, Hagan *et al.* 1996, Donovan *et al.* 1997, Bayne et Hobson 2001, Schmiegelow et Mönkkönen 2002). Dans ce type de milieu, les oiseaux forestiers ne peuvent pas utiliser la matrice pour combler leurs

besoins. De ce fait, les caractéristiques des peuplements résiduels et la quantité/qualité d'habitats dans le paysage adjacent jouent un rôle très important. Toutefois en milieu forestier, les effets de l'environnement adjacent sont mitigés selon plusieurs études, tant du point de vue de la composition en espèces (c.f.: Lichstein *et al.* 2002) que de la reproduction des oiseaux (c.f.: Schmiegelow et Mönkkönen 2002). Notre étude ainsi que la majorité des études précédentes ont caractérisé le paysage dans un rayon de 500 m à 2 km de rayon (Drapeau *et al.* 2000, Lichstein *et al.* 2002, Betts *et al.* 2007, St.-Laurent *et al.* 2007). Beaucoup ont justifié leur choix en fonction de la taille des territoires des espèces étudiées (voir: Mazerolle et Villard 1999). Or, il a été montré que les oiseaux peuvent se disperser sur plusieurs dizaines de kilomètres (Tittler *et al.* 2009) et que leur distance de dispersion peut augmenter dans des paysages plus fragmentés (Tittler *et al.* 2006). Les oiseaux pourraient être ainsi affectés par les caractéristiques du paysage à de multiples échelles. De plus, la nature de la matrice à une échelle donnée pourrait résorber ou amplifier les effets de la perte d'habitat à une autre échelle (McGarigal et McComb 1995). Ces aspects montrent alors l'importance d'étudier les effets de la fragmentation sur les populations animales en utilisant les caractéristiques locales de l'habitat, celle du paysage, mais également les caractéristiques régionales du territoire.

La fragmentation à l'échelle régionale

Les territoires aménagés diffèrent selon leurs caractéristiques physiques (ex. : relief, hydrologie, etc.) et leur utilisation (foresterie, agriculture, etc.), mais également en fonction de leur historique d'aménagement. Ces facteurs peuvent influencer la réponse des oiseaux aux modifications du paysage. Un territoire comme la Haute-Mauricie a été majoritairement aménagé à des fins de foresterie depuis plus d'un siècle (Alvarez 2009). Le paysage accidenté a fait en sorte que les parterres de coupe y sont majoritairement petits et découpés. Les perturbations naturelles sont également très présentes dans la région (Alvarez 2009). En effet, à 136 ans le cycle des feux est modéré par rapport à d'autres régions du Québec (Lesieur *et al.* 2002, Bergeron *et al.* 2006) et les épidémies d'insectes, fréquentes (Alvarez 2009). Leurs effets non négligeables sur la structure de la matrice forestière s'ajoutent à ceux de la foresterie. Bien que ces perturbations affectent significativement la matrice, cette dernière reste de nature forestière. Or, les résultats obtenus dans cette matrice peu hostile (55 % de forêts de 7 à 12 m) ne sont pas

nécessairement généralisables dans d'autres régions où l'aménagement peut être plus intensif (ex. : plus grands parterres de coupe) dans des écosystèmes moins productifs (ex. : en pessière à mousses) qui mettent plus de temps à se régénérer. Dans ces milieux, il serait possible que la densité d'oiseaux associés aux forêts matures et leur reproduction soient davantage affectées par les coupes. Cette hypothèse peut-être difficile à vérifier à cause de l'échelle étudiée et du manque de connaissances sur la variété d'habitats utilisés par les différentes espèces forestières. Il faudrait également tenir compte des effets de la composition et configuration du paysage à différentes échelles sur les populations d'oiseaux, ainsi que les interactions qu'il pourrait y avoir entre les échelles.

Recommandations

Il a déjà été proposé d'établir des seuils auxquels les effets de la fragmentation peuvent avoir une influence notable sur les communautés animales ou sur une espèce focale (Andrén 1994, Mönkkönen et Reunanen 1999). De telles informations seraient très utiles aux gestionnaires, car ils pourraient ainsi mieux juger les effets ou les conséquences de l'aménagement d'un territoire. Toutefois, tel que montré dans cette étude, les effets de perte d'habitat sur les communautés d'oiseaux et la reproduction des espèces doivent tenir compte de la nature de la matrice et de l'échelle étudiée. Un territoire constitué d'habitats résiduels enclavés dans une matrice de coupes en régénération de moins de deux mètres de hauteur n'offre pas les mêmes conditions de dispersion aux oiseaux de forêts matures qu'un territoire où la matrice est dominée par des jeunes peuplements de 7 à 12 m, comme c'est présentement le cas en Haute-Mauricie. Ces seuils d'habitat sont alors dépendants de la nature de la matrice transformée par l'activité humaine. Il est alors difficile d'identifier ces seuils, car il serait nécessaire de tenir compte des caractéristiques de la matrice à plusieurs échelles. Les seuils définis doivent être adaptables aux caractéristiques des matrices des régions et seront probablement variables selon l'échelle et les espèces étudiées. Dans le cadre de gestion de territoires, il faudra alors utiliser ces seuils avec précaution et préconiser des analyses multi-échelles spécifiques à chaque territoire concerné.

Pour l'étude de la reproduction des oiseaux forestiers, le Roitelet à couronne dorée a été choisi comme espèce focale en raison : (1) qu'il est associé aux forêts âgées en forêt boréale (Drapeau *et al.* 2003), (2) qu'il est reconnu comme étant sensible aux perturbations de son habitat (Guénette et Villard 2005, Venier et Pearce 2005, Stuart-Smith *et al.* 2006, St-

Laurent *et al.* 2008) et, (3) de la possibilité d'acquérir des connaissances sur un effectif suffisamment élevé d'individus pour mener des comparaisons statistiques (c.-à-d. : grande occurrence, petite taille des territoires de reproduction). Nos résultats ont montré que cette espèce migratrice de courte distance pouvait avoir un succès de reproduction élevé dans des habitats résiduels isolés, mais il est possible que les espèces résidentes puissent être davantage affectées par les modifications de leur habitat que ne le sont les migrateurs (Imbeau *et al.* 2001, Schmiegelow et Mönkkönen 2002). Les picidés, entre autres, pourraient être particulièrement sensibles à cause de la taille de leur territoire nécessaire pour leur reproduction et leur nutrition. Au cours de leur cycle de vie, plusieurs dépendent du bois mort disponible dans leur habitat (Imbeau *et al.* 2001). Or, comparativement aux perturbations naturelles, l'aménagement forestier a pour conséquence de diminuer la quantité de bois mort dans le paysage (Drapeau *et al.* 2009). Ainsi, les pics pourraient constituer des espèces focales intéressantes pour vérifier les effets de la fragmentation du paysage. Toutefois, l'étude des données de repasse de chants du premier chapitre n'a pas permis de trouver des relations entre la fragmentation du paysage et l'occurrence des pics, ainsi que pour d'autres espèces particulièrement sensibles. Encore, ces résultats sont probablement dus à la nature de la matrice forestière.

Dans cette étude, il n'a pas été possible d'établir de relations fortes ou des seuils entre les variables du paysage et la structure des communautés d'oiseaux ou avec le succès de reproduction d'une espèce associée aux forêts matures. Cela ne suggère pas toutefois qu'un aménagement plus intensif de l'ensemble du territoire, où l'on fragmenterait davantage le paysage, permettrait de maintenir les communautés d'oiseaux associées aux forêts matures. En effet, un changement dans la composition de la matrice forestière régionale, notamment un accroissement significatif de parterres de coupes en régénération (< 3 m), pourrait affecter les communautés puisque le paysage deviendrait davantage similaire à un paysage agroforestier. Si tel est le cas, un aménagement plus intensif pourrait alors entrainer une diminution de la capacité des peuplements résiduels à remplir leur rôle de maintient des communautés animales.

Pour être en mesure de vérifier l'influence de la matrice forestière à l'échelle régionale sur les communautés d'oiseaux et leur reproduction, il serait nécessaire de comparer plusieurs régions forestières entre elles où les proportions de parterres de

régénération (0-3 m), de forêts en régénération (3-7 m), de jeunes forêts (7-12 m) et de forêts matures (>12 m) pourraient varier. Par exemple, il serait possible de vérifier si la structure des communautés est similaire entre deux régions ayant des niveaux de fragmentations différents. Un échantillonnage stratifié de plus petits paysages dans chaque région permettrait de vérifier la présence d'interactions entre les échelles. Plusieurs espèces focales pourraient alors y être échantillonnées. Pour être en mesure de mesurer les effets de la perte d'habitat sur ces espèces, il serait préalablement nécessaire de caractériser les habitats utilisés par celles-ci et leur niveau d'utilisation (voir Betts *et al.* 2007). Cette caractérisation permettrait entre autres d'acquérir des connaissances sur le rôle fonctionnel des jeunes forêts pour les oiseaux forestiers.

Conclusion

Cette étude aura montré que les peuplements résiduels, d'une forêt aménagée boréale mixte, ont des communautés d'oiseaux semblables à celles que l'on trouve dans des massifs forestiers et que leur reproduction ne semble pas y être compromise, et ce, dans un contexte où seulement 10 % de la région à l'étude était constituée de forêts matures. Ce résultat étonnant met toutefois en perspective le rôle potentiel des jeunes forêts qui constituaient 55 % du couvert forestier du territoire et qui sont vraisemblablement des habitats qui permettent la dispersion des oiseaux des forêts matures dans les habitats résiduels. Le rôle écologique de ces habitats pour les oiseaux forestiers reste donc à évaluer. Les peuplements résiduels semblent donc constituer de bons habitats pour les oiseaux forestiers et leur conservation est importante dans les paysages aménagés.

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